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Environmental Factors Affecting Loggerhead Sea Turtle (Caretta caretta) Nesting, Hatching, and Incubation Patterns in Broward County, Florida

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ENVIRONMENTAL FACTORS AFFECTING LOGGERHEAD SEA TURTLE (*CARETTA CARETTA*) NESTING, HATCHING, AND INCUBATION PATTERNS IN BROWARD COUNTY, FLORIDA

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Zoey Ellen Best

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Abstract

Reproductive success in loggerhead (*Caretta caretta*) sea turtles is strongly dependent on the effective placement and internal conditions of their nests. Embryos rely on optimal incubation conditions for proper development and growth, which determines how many hatchlings will emerge from the nest. The internal microclimate of each nest is delicately balanced and can be easily influenced by external environmental conditions. This study was designed to examine several environmental variables and determine their effects on sea turtle nesting numbers, hatching success, and incubation conditions in Broward County Florida. Over a span of 25 years (1991-2015), the Broward County Sea Turtle Conservation Program has collected data on each sea turtle nest laid in Broward County. This data was analyzed and plotted to visualize nesting and hatching trends, and regressions were fitted to make comparisons to historic air temperature, sea surface temperature, precipitation, and lunar illumination data. These regressions were tested for significance, and each environmental variable was found to have varying levels of impact on sea turtle nesting and hatching behavior. Of the environmental variables considered in this study, analyses suggest that sea turtles are most responsive to temperature, with sea surface temperature serving as the best proxy for predicting nesting behaviors. Air temperature over the incubation period was found to be the best indicator for hatch success percentage. Air temperature, sea surface temperature, and precipitation averages all significantly affected the length of the incubation period. The regression models created in this study could be used to examine the interactions between climatic variables, and to indicate what impacts can be expected by these various environmental factors. This information could be used to estimate the future effects of climate change on sea turtle reproduction, and to predict general reproductive success and future population trends.

Keywords: Sea Turtle, Loggerhead, *Caretta caretta*, Nesting Behavior, Hatch Success, Air Temperature, Sea Surface Temperature, Precipitation, Lunar Phase, Moon Illumination, Marine Biology, Broward County

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Introduction

Nesting behavior is a complex component of a female sea turtle's life history, with major impacts on her reproductive fitness. Successful nesting requires the female to locate her natal beach, ascend the sand, excavate an egg chamber, deposit her eggs, and ensure that the nest is buried and camouflaged (Miller et al., 2003; Wood and Bjorndal, 2000). As oviparous species with no parental care, sea turtle reproductive success is dependent on the female to select an appropriate nest site for her developing offspring (Broderick et al., 2001; Huang and Pike, 2011; Wood and Bjorndal, 2000). The nesting beach serves as an incubator for the embryos, which are profoundly affected by the quality of their incubation conditions (Ackerman, 1997; Broderick et al., 2001; Rafferty and Reina, 2014). Sea turtle eggs need adequate humidity, salinity, respiratory gases, and temperature for normal development, which can only be supplied by their local environment (Ackerman, 1997). Therefore the spatial and temporal placement of each clutch, as well as the proficiency of the female's nesting activities, is critical for her reproductive success (Huang and Pike, 2011; Miller et al., 2003; Rafferty and Reina, 2014).

The conditions within each sea turtle nest are delicately balanced, requiring moderate and stable surroundings to foster a suitable nest environment. The local climate, physical structure of the beach, and metabolic processes of the embryos interact to form a microclimate within the nest (Ackerman, 1997). This microclimate regulates embryonic development and insulates the eggs from external environmental conditions (Broderick et al., 2001; Huang and Pike, 2011). Under ideal circumstances the parameters of the microclimate are in equilibrium, creating a paragon environment for successful incubation. However extended periods of extreme environmental conditions, such as high sand temperatures or excessive rainfall, can upset the nest microclimate. (Broderick et al., 2001). The embryos are physically incapable of escaping their nest environment during incubation, so they are at an increased risk of physiological stress if the nest conditions become unfavorable (Drake and Spotila, 2002; Pike, 2014). While some oviparous species have been known to exhibit behavioral and physiological plasticity in response to environmental stressors, the extent of these capabilities is unknown in sea turtles (Du and

Shine, 2015). Therefore developing sea turtle embryos could be considered fundamentally vulnerable and susceptible to their local climate conditions.

ENVIRONMENTAL EXAMINATION

Environmental conditions are controlled by a host of climatic variables. While temperature is often cited as one of the most prominent factors affecting sea turtle reproduction, it is one of many interacting climatic variables that have been known to impact sea turtle life histories (Harley et al., 2006). The onset of the sea turtle nesting season is strongly influenced by the turtles' local environment, and they use multiple environmental factors as cues to determine when they will come ashore to nest (Pike, 2008). These same environmental factors can have a significant effect on the internal nest environment on the beach, which directly translates to embryo development and the resulting hatching success. Considering this strong relationship between the environment, nest conditions, embryo development, and hatching success, environmental quality has been shown to provide a strong measure of reproductive output in some loggerhead sea turtle populations (Pike, 2014).

While climatic conditions can have significant independent effects on sea turtle reproduction, their complex interactions can also complicate these results. Taking into account location, time, seasonality, and patterns of change, the biological responses to these environmental factors can be enigmatic (Harley et al., 2006). Environmental variables are often highly correlated, which can make the impression of a single variable difficult to isolate (Pike, 2008). The cumulative effect of multiple stressors may either augment or reduce the expected biological response when compared to a single stressor, so it is important to consider these compounded effects during statistical analyses (Harley et al., 2006; Pike, 2008). Nonetheless, the most prominent environmental variables affecting sea turtles have all been statistically linked to multiple components of their life history, and are therefore primary candidates for analysis.

Air Temperature

Air temperature is a common proxy for general temperature trends that has been previously linked to sea turtle reproductive behavior. Many studies have demonstrated that the nesting behavior of multiple oviparous species is governed by the magnitude and extent of spring temperatures (reviewed in Crick and Sparks, 1999). These oviparous species have been known to shift their nesting seasons forwards or backwards to align with temperature patterns in order to nest in ideal temperature conditions (Pike, 2006). Specifically with respect to sea turtles, principal component analysis by Pike (2008) of multiple environmental variables demonstrated that air temperature had a coefficient above 0.80 for a principal component explaining nearly 30% of nesting variation in a sample of sea turtle nests from Central Florida.

Air temperature is also an important variable that significantly affects nest temperature and incubation conditions. Ambient air temperature is highly correlated with daily sand temperature, which is a strong indicator of internal nest temperature (Hays et al., 1999; Huang and Pike, 2011). Air temperature has a direct positive relationship with nest temperature, such that higher air temperatures result in higher sand temperatures and higher nest temperatures (Girondot and Kaska, 2015). What's more, threshold sand temperatures appear to be the primary cue that hatchlings use to determine appropriate timing of emergence from the nest (Drake and Spotila, 2002). Considering the profound effect that incubation conditions have on the development of embryos and success of hatchlings, air temperature can be broadly linked to total hatching success (Pike, 2014; Rafferty and Reina, 2014).

Sea Surface Temperature

Similarly to air temperature, sea surface temperature is also a representation of the temperature trends that have been linked to sea turtle life history patterns. Warming ocean temperatures at both foraging grounds and nesting beaches can elicit the onset of the sea turtle nesting season each year (Pike, 2008). In some studied locations, years with warmer spring sea surface temperatures resulted in the advancement of the nesting season to align with ideal nesting temperatures (Mazaris et al., 2008; Pike et al., 2006). Additionally, sea surface temperatures have been related to nesting abundance and nesting season length (Chaloupka et al., 2008; Hawkes et al., 2007; Mazaris et al., 2008; Pike et al., 2006; Weishampel et al., 2010). Higher sea surface temperatures in sea turtle foraging grounds can result in lower nesting abundance in the following season, and the results of increased sea surface temperature on nesting season length is varied (Chaloupka et al., 2008). Hawkes et al. (2007) in North Carolina and Mazaris et al.

(2008) in Greece both found that increased spring sea surface temperatures resulted in increased nesting season duration, while Pike et al. (2006) found that increased sea surface temperature actually decreased nesting season duration in Florida.

Additionally, sea surface temperature is also a successful proxy for sand temperatures, nest temperatures, and incubation conditions. Sea surface temperature and air temperature are typically highly correlated, and higher sea surface and air temperatures also indicate higher nest temperatures (Girondot and Kaska, 2015). The solar irradiation that influences circulation and heating affects sea surface temperature and sand temperature in similar ways, such that sea surface temperature is a strong predictor for nest temperature (Girondot and Kaska, 2015). One study by Fuentes et al. (2009) included sea surface temperature as a covariate for air temperature, allowing them to create a regression model that was able to explain up to 94% of the variation in nest sand temperatures. Due to the strong relationship between nest temperature and embryo development, this also makes sea surface temperature an indicator of hatching success and reproductive output.

Precipitation

Precipitation is another environmental factor that can help predict sea turtle reproductive patterns. Pike (2008) found that the number of nests laid in Central Florida was positively associated with rainfall in a principal component analysis, but other studies have shown that excessive rainfall is thought to discourage sea turtle nesting (Dodd, 1988). Conversely, a significant lack of precipitation can also have negative effects on nesting numbers. Arid conditions can cause beach sand to be excessively dry and crumbly, reducing the female's ability to successfully dig her nest (Margaritoulis, 2005). Thus, it seems as if a moderate or normalized level of precipitation is most conducive to successful nesting and a maximization of nests laid.

After the nest is laid, the eggs continue to rely on precipitation levels for idealized microclimate conditions (Ackerman, 1997). Newly laid eggs absorb water from the nest sand in order to become turgid, and they continue to require a surrounding moisture level of around 25% for maximum optimization of growth, development, and hatching success (McGehee, 1990; Miller et al., 2003). Excessive precipitation greatly increases the water content of the sand surrounding the eggs, which can be detrimental to the developing embryos. Inundation from rainfall reduces ventilation and gas exchange, which can cause developing embryos and unemerged hatchlings to suffocate from the limited oxygen supply (Kraemer and Bell, 1980; Miller et al., 2003; Margaritoulis, 2005; Patino-Martinez et al., 2014). Excessive rainfall can also have a cooling effect on ambient sand temperatures, affecting the internal nest microclimate and potentially slowing development and increasing incubation periods (Kraemer and Bell, 1980; Matsuzawa et al., 2002). However without enough rain, the converse is true and the embryos can overheat and perish or the nests can collapse entirely (Valverde et al., 2010); Saba et al., 2012). This supports the idea that an intermediary level of precipitation is most ideal for sea turtle nest health.

Lunar Illumination

While lunar illumination is not an environmental factor in the same sense as the previous variables, it is a commonly cited environmental condition that has been known to affect the reproductive behavior of many marine species. Many marine invertebrates have rhythmic patterns of locomotion, molting, and reproduction that all coincide with lunar phases (Naylor, 1999). A synopsis by Dodd (1988) found a study reporting a positive correlation between sea turtle nest numbers and the period of the full moon [Uchida, 1981], as well as several studies reporting no such relationship [Caldwell, 1959; Iwamoto et al., 1985; Routa, 1968]. A more recent study also found a positive relationship between moon cycles and the timing of sea turtle nesting (Barik et al., 2014). This relationship could be a function of the portion of the moon that is illuminated, or of the tidal cycles that coincide with the lunar phases (Naylor, 1999; Pike, 2008). Therefore lunar phase and illumination should be analyzed carefully when determining how and whether it significantly affects sea turtle nesting.

Objectives

The Broward County Sea Turtle Conservation Program has been collecting data on loggerhead sea turtle nests in subtropical South Florida for the past 25 years, providing a comprehensive account of sea turtle emergences and nests in this area since 1991. The BCSTCP Database contains information on each false crawl and nest event from 1991-2015, including the lay date, species, location, and hatch date (as well as an egg count and hatchling success when available). From this data, overall fecundity and incubation period can be calculated and examined. In conjunction, air temperature, sea surface temperature, precipitation, and lunar illumination have all been selected as environmental variables that are expected to have a significant impact on sea turtle nesting behaviors and reproductive success. These variables have been monitored consistently in South Florida during the study period of 1991-2015, and are therefore ideal candidates for comparison in this study.

By examining the relationship between daily environmental parameters and individual nest data, this study serves to determine what role the local environment plays in the reproductive performance of sea turtles. Comparing nesting, hatching, and incubation patterns to local environmental data will demonstrate how concurrent climate conditions affect sea turtle reproduction both within and across seasons. Considering the interrelated nature of climate parameters and sea turtle life history patterns, the selected variables are likely to have a definable impact on the sea turtle nests of Broward County. The relationships between the selected environmental variables and the reproductive patterns of loggerhead sea turtles should be visible in both short and long-term analyses, and will also help predict the long-term effects of climate change in these areas.

Therefore the objectives of this study can be summarized as follows:

1. To evaluate the nesting and hatching patterns of loggerhead sea turtles in Broward County over a 25-year span
2. To create regression models using environmental factors to predict seasonal nesting, hatching, and incubation trends
3. To examine these models to evaluate the potential impacts of climate change on local sea turtle populations

Materials and Methods

SEA TURTLE SPECIFICS

Broward County is a common nesting site for loggerhead, green, and leatherback sea turtles. Broward County lies between Palm Beach County and Miami-Dade County, and spans 38.6 kilometers of Florida's southeastern coast (Figure 1). As of 2015, Broward County accounted for approximately 2.8% of all sea turtle nests occurring on Florida's East Coast (Florida Fish and Wildlife Commission, 2015).

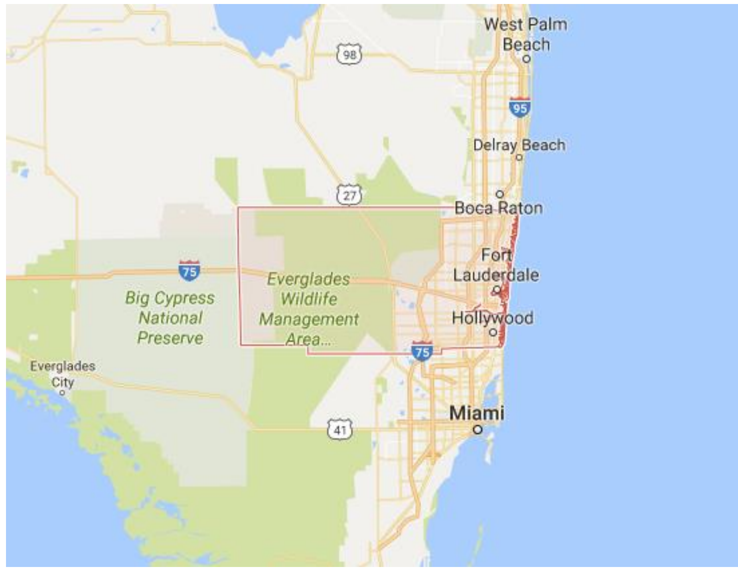

Figure 1: Broward County Florida

The Broward County Sea Turtle Conservation Program is responsible for monitoring the beaches of Broward County (with the exception of the Dr. Von D. Mizell-Eula Johnson State Park) each morning throughout the potential nesting season from March 1st to October 31st. These surveys may consist of identifying fresh sea turtle tracks, locating and staking off new nests, and excavating post-emergence egg chambers. When a new nest is located, a GPS is used to record the exact location of the egg chamber. The species of the mother is determined by the crawl characteristics, and notes are taken on the general status of the nest. Once the nest has hatched, it is excavated and the remaining contents of the nest are examined. If after 70 days (80 days for leatherbacks) the nest still has not hatched, it will be excavated and the contents analyzed. With permission from the Florida Fish and Wildlife Conservation Commission (FWC) and Broward County, the BCSTCP has provided comprehensive datasets from the past 25 years of nest surveys for this study. The different analyzable variables from each nest laid from 1991-2015 can be seen in

. Additionally, the counts of total false crawls for each day of the nesting season were available starting in 1992. Due to surveyor error, there is a possibility that a small number of false crawls were marked as nests and nests were marked as false crawls. However it is likely that this type of error was so infrequent that it would not have any significant effect on statistical analyses. Although all variables were recorded for all three local species of sea turtle, the profusion of loggerhead nest data with respect to the other species made them ideal for a large-scale statistical analysis. Therefore loggerhead sea turtles will be the only species considered for the remainder of this study.

Table 1: Analyzable variables for sea turtle nests laid in Broward County Florida

Variable	Parameter
Year	1991-2015
Species	Loggerhead, Green, or Leatherback
Latitude	°N (Positive)
Longitude	°W (Negative)
Zone	R1-R128. 305-meter-long zones running the length of Broward County
Date Laid	Date of egg deposition
Relocation Status	Yes or No. Whether the nest was relocated after egg deposition
Chamber Depth	Depth to the bottom of the egg chamber in centimeters
Track Width	Width of the tracks leading up to the nest in centimeters
Hatch Date	Date of first hatchling emergence
Incubation Period	Total number of days between egg deposition and hatchling emergence
Egg Number	Total number of hatched and unhatched eggs in the nest
Hatchlings Released	Total number of living hatchlings released into the ocean
Eggs Lost	Total number of eggs predated, destroyed, or lost
Hatch Success Percentage	Number of hatched turtles divided by the total number of eggs in the nest
Nest Condition	Hatched or Unhatched; Predated or Non-predated; Washed away or Intact. Objective notes on the status of the nest
Egg Development	Live pipped egg, dead pipped egg, live in nest, dead in nest, visual development, no visual development, or white. Condition of each embryo or hatchling remaining in the nest

External Elements

Air Temperature and Precipitation

Air temperature and precipitation data for Broward County were retrieved from National Oceanic and Atmospheric Administration's (NOAA) National Climatic Data Center. A daily summary of climatic data included minimum and maximum air temperatures, average wind speed, precipitation, and total sunshine. All climatic data points were collected by the Fort Lauderdale, FL station at 26.1019° latitude, -80.2011° longitude. This station was chosen due to its central location within Broward County and its continuous record of climatic data throughout the study period, which ensured consistency from year to year. Daily air temperature average was calculated in °C from the minimum and maximum air temperatures each day, and daily precipitation was recorded in centimeters per day.

Sea Surface Temperature

High-resolution optimally interpolated sea surface temperature data was collected from NOAA's Earth System Research Laboratory Physical Sciences Division. The downloaded Advanced Very High Resolution Radiometer (AVHRR) data included the daily mean sea surface temperature within a range of latitudes from 26° to 26.25° and longitudes -80.5° to -80° (Figure 2). These sea surface temperature values were recorded on a scale of 0.25° latitude and longitude. This prevented the analysis of any values further inshore, as the obstruction of the Florida coast rendered these data points non-applicable. Therefore the

selected area is the most accurate representation of the sea surface spanning the Broward County coast. The average sea surface temperatures in this area from 1991-2015 were downloaded in a NetCDF file, and then converted to quantifiable data in R version 0.99.903 with the ncdf4, chron, RColorBrewer, and lattice packages.

Lunar Illumination

Lunar data throughout the 25-year study period was downloaded from the United States Naval Observatory (UNSO) website. A UNSO data service was used to calculate the fraction of the moon illuminated on each night from 1991-2015. This resulted in a single value for each day, recorded as a percentage (hereafter referred to as lunar fraction). From this data, the lunar phases were assigned by separating the 29.5-day lunar cycle into four equal parts (hereafter referred to as lunar phase). Lunar fractions from 0 to 0.17 were assigned as New Moons, and lunar fractions from 0.87 to 1 were assigned as Full Moons. All lunar fractions from 0.18 to 0.86 were assigned as Waxing if they followed a New Moon, and Waning if they followed a Full Moon. This ensured approximately 7 days were relegated to each phase of the moon, with each phase garnering the occasional 8th day in approximately equal proportions.

Statistical Scrutiny

Descriptive Statistics

From the comprehensive sets of environmental and sea turtle nest data, a series of descriptive statistics were created to analyze patterns within and between years. The average number of nests and false crawls per day were calculated from year to year and across the seasons, and the net totals for each year were summed. The mean and median nesting date were calculated from the aggregate of these nesting events. Similarly, the average number of hatched nests per day was also calculated from year to year and across the seasons, as well as the mean and median hatch date. From the first and last date of emergence the length of the nesting season was calculated, and from the first and last date of hatching the length of the hatching season was calculated. The average hatch success percentage was calculated from year to year and across the seasons, as was the average length of the incubation period.

Statistical Tests

Similarly to the descriptive statistics, each measurable component of the sea turtle nesting season (nests laid, hatch success percentage, incubation period length, etc.) was first plotted with respect to each environmental or temporal variable. Based on the linear and curvilinear shapes of these plots, each graph was then fitted with either a linear or 2^{nd} order polynomial regression line. In most instances the shape of the plot gave clear indication of the appropriate model of fit; however some plots were fitted with both a linear and a polynomial regression line, and the model with the higher R^2 value was kept.

The total number of nests laid each day and nests hatched each day were first plotted against Julian date, in order to demonstrate the general nesting and hatching trends throughout the loggerhead nesting season. 2^{nd} order polynomial regression lines were the ideal fit for both the plots of nesting events and hatching events compared to their respective Julian dates. The number of nests laid each day was then compared to the average daily values of air temperature, sea surface temperature, precipitation, and lunar fraction. The resulting R^2 values of these regressions (two 2^{nd} order polynomial models and two linear models respectively) were utilized to determine what proportion of nesting variance could be determined by each individual environmental variable. The average hatch success percentage of each nest was also plotted and compared to air temperature, sea surface temperature, and precipitation, although these environmental variables were measured over the average length of the incubation period prior to the hatch date. These averages were calculated to account for the typical environmental conditions over the incubation period of each nest, and 2^{nd} order polynomial regression models and linear models were fitted to determine how average environmental conditions individually affected hatch success percentage. Additionally, hatch success percentage was plotted against the lunar fraction of the hatch date and a linear model was fitted to determine whether the illumination of the moon affected when a nest would hatch.

After the individual regression models were completed, two multiple regression analyses were conducted to compare nests laid and hatch success percentages to the composite of all four environmental variables and each of their interactions. Considering the curvilinear shape of almost all of the individual regressions, a 2^{nd} order polynomial model was used to fit the multiple regression. Nests laid were evaluated with respect to daily environmental values, while hatch success percentage was evaluated with respect to average environmental values over the incubation period, in addition to daily values of air and sea surface temperature. Each model was initially crafted to include every environmental variable, the square of each variable, and the interactions between every combination of the variables and their squares. Then stepwise removal was utilized for both multiple regression models to ensure parsimony. Variables and interactions with p-values less than 0.05 were first eliminated from the original model, and a new model was created. The original and new models were compared using an ANOVA test, and assuming the difference between the two models was statistically insignificant, the newer model was kept. This process was repeated with the least significant variables or interactions being removed one by one until the difference between models was statistically significant via an ANOVA test. The most parsimonious model that was still statistically similar to the original model was chosen as the final model to represent environmental impact on nests laid and hatch success percentage, and these models are presented in the results. Stepwise addition was also used in an attempt to create parsimonious models, but the results did not improve compared to the stepwise removal method so they are omitted for brevity. All nesting regressions were also completed with respect to false crawls, but the results are omitted for brevity considering the high correlation between nests laid and false crawls (Appendix: Figure 10).

Additionally, to examine environmental effects on incubation, the incubation period for each nest was plotted with respect to its lay date and hatch date and a 2^{nd} order polynomial regression line was fitted to each plot. Regression analyses were completed to compare the length of the incubation period to the hatch success percentage of each nest, and to compare the length of the incubation period to average air temperature, average sea surface temperature, and precipitation over the average incubation period. This demonstrated how environmental conditions throughout the incubation period affected its total length. Kendall’s rank correlation tests were also conducted to examine the relationships between air temperature, sea surface temperature, and precipitation over the incubation period.

All data analysis was performed in R using the packages car, lme4, plyr, and zoo. Additional analyses of the completed regression models were computed by hand. To determine the maximum values of the polynomial regressions, the first derivative of the functions were taken and solved for 0. To determine the net rate of change over the regressions, the maximum and minimum integer values were entered into the function and the difference between the results was divided by the difference between the integers. While this method was not able to account for the curvilinear shape of the regressions (and therefore constantly changing derivatives), it was determined to be the best approximation for summarizing the constant rate of change.

All data entries from all years were included in each statistical analysis. Entries were only excluded from individual tests if data was insufficient to conduct the appropriate analysis.

Results

Throughout the nesting seasons from 1991-2015, the average number of nests laid per day was found to be 16.98 with a standard deviation of 12.94. The average number of false crawls per day from 1992-2015 was 19.55 with a standard deviation of 18.55. The total number of nests laid and false crawls combined (hereafter referred to as emergences) varied significantly from year to year. However a significant decline in emergences was recorded from 2001-2007, followed by a gradual increase back to previous levels (Appendix: Figure 11 - Figure 12). Throughout the hatching season, the average number of nests hatched per day was found to be 13.93 with a standard deviation of 11.52. There were no significant relationships or noticeable trends between the year and the first emergence date, mean nesting date, median nesting date, mean hatch date, median hatch date, nesting season length, or hatching season length (Appendix:

Figure 13 - Figure 19). The average length of each incubation period was 50.55 days, and the average hatch success was 71.02%. A yearly summary of each of these nesting and hatching variables can be seen in Table 2 and

of the Appendix.

NESTING NUMBERS

A strong curvilinear relationship was visible between Julian date and nests laid, suggesting fewer nesting events towards the beginning and end of the season and peak nesting occurring towards the middle of the season (Figure 3). A similar pattern appeared in the graph of sea surface temperature compared to nests laid, which explained 23.3% of the variation in sea turtle nesting numbers (

Figure 4). The parabolic polynomial regression suggested that both low and high values of sea surface temperature result in the lowest numbers of nests, and mid-range sea surface temperature values produce the highest numbers of nests. The ideal mid-range sea surface temperature for the maximum number of nests was 28.11°C. The individual regression models comparing nests laid to average air temperature, precipitation, and lunar fraction resulted in much weaker or insignificant relationships (Appendix:

Figure 20 - Figure 22). However including these remaining variables and their interactions in the multiple regression model slightly increased the explanation of

variation to 26.2%. A summary of the coefficients for the most parsimonious multiple regression model can be seen in Table 4 of the Appendix.

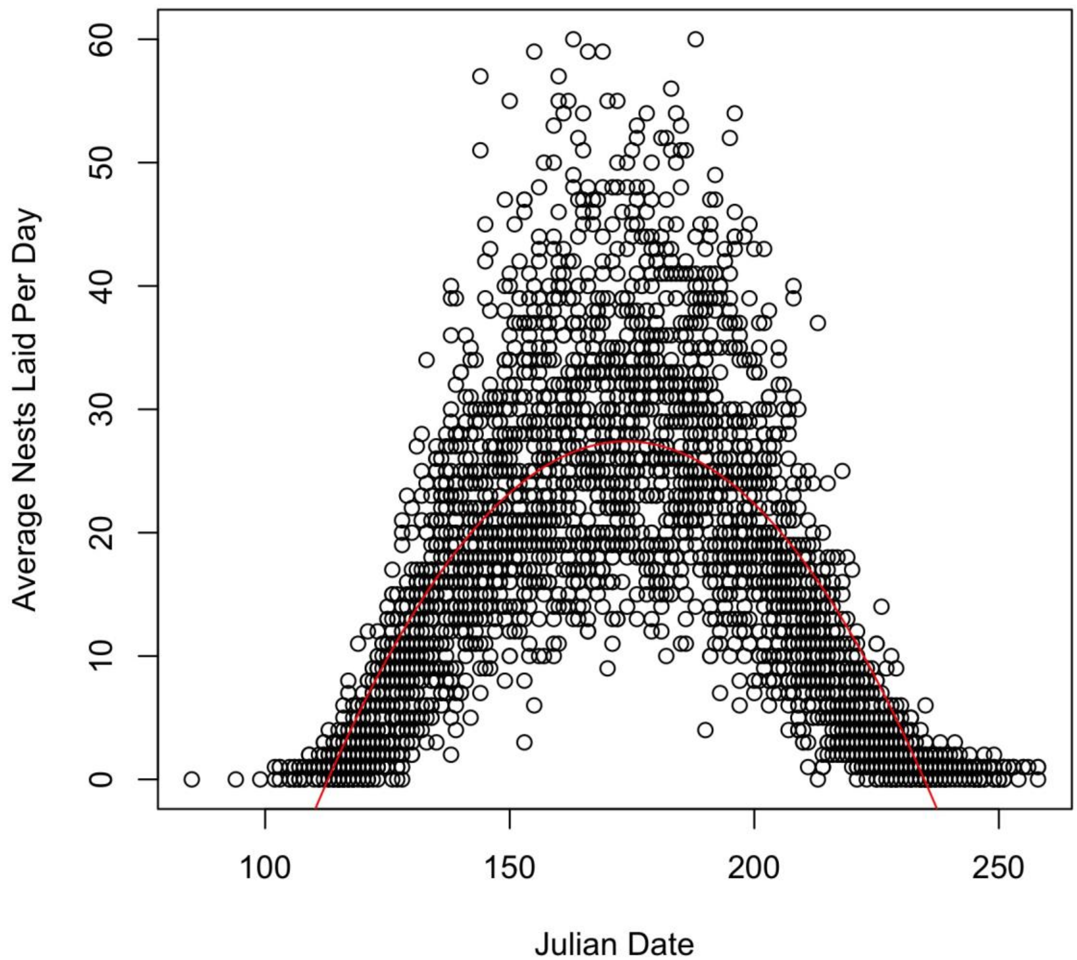

Figure 3: Average loggerhead nests laid compared to Julian date from 1991-2015. Polynomial model: $y = -0.007X^2 + 2.565X - 195.5$, $R^2 = 0.598$, $p < 0.001$

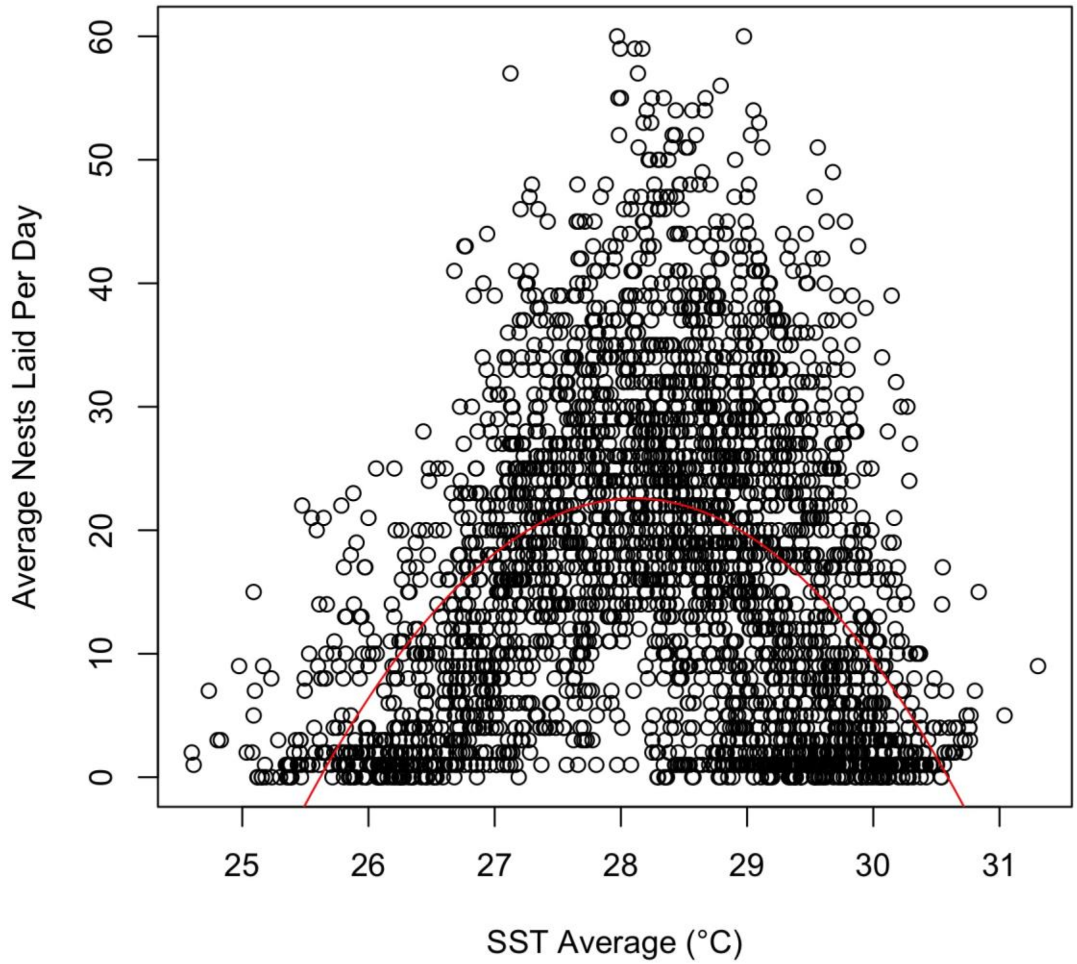

Figure 4: Average loggerhead nests laid per day compared to daily average sea surface temperature (°C).
Polynomial model: $y = -3.654X^2 + 205.401X - 2{,}863.739$, $R^2 = 0.233$, $p < 0.001$

HATCHLING HAPPENINGS

A strong relationship was also visible between Julian date and the number of nests hatched (**Figure 5**). The relationship demonstrated a similar curvilinear trend to nests laid, however with a lower R^2 value (0.339 rather than 0.598). The curvilinear model for air temperature average had the strongest impact on hatching success, explaining the most variation (21.0%) in hatch success percentage

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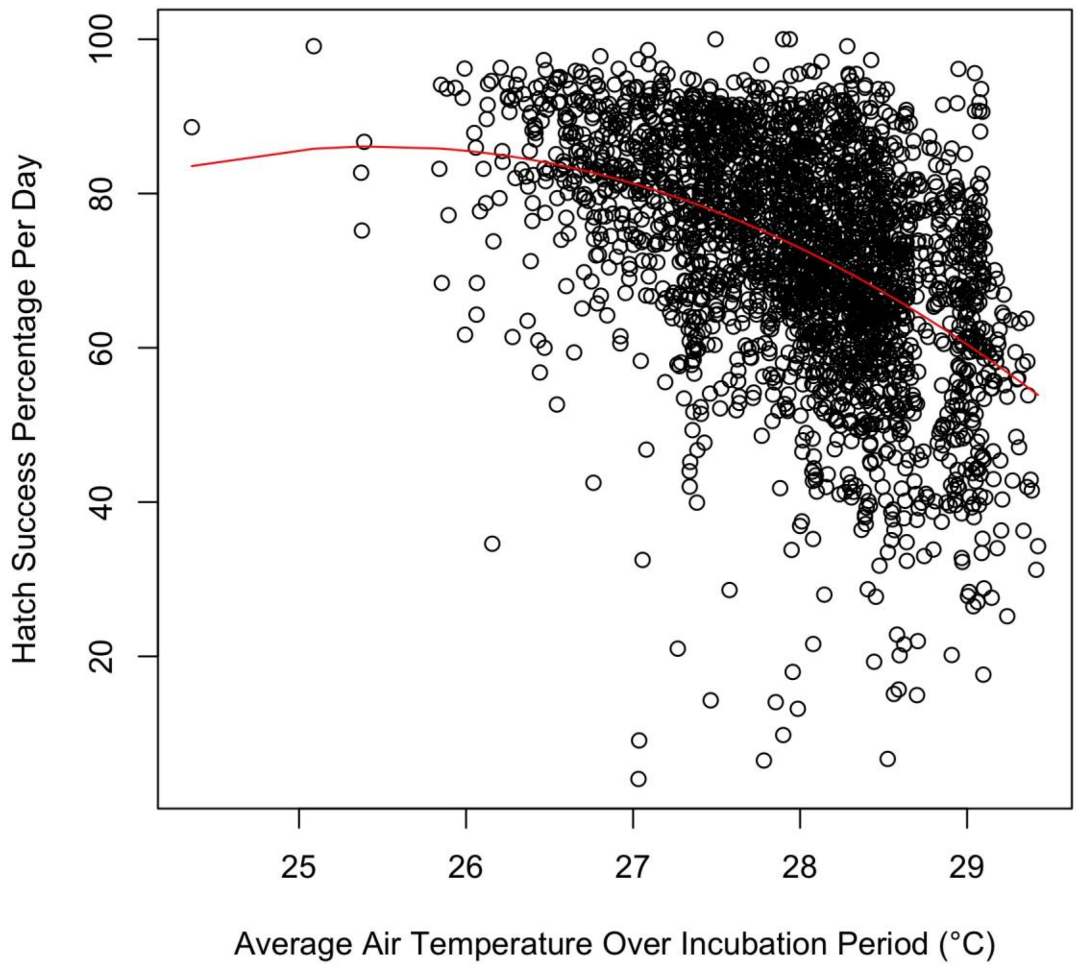


Figure 6). The ideal air temperature average over the incubation period for peak hatching success was 25.47°C, suggesting that warmer temperatures over the 51 days prior to hatching significantly reduced the hatch success percentage of loggerhead nests. Similarly to nesting success, the individual regression model comparing hatch success percentage to sea surface temperature demonstrated a moderate relationship, while the relationships to precipitation and lunar fraction were weak or insignificant (Appendix: **Figure 24** -

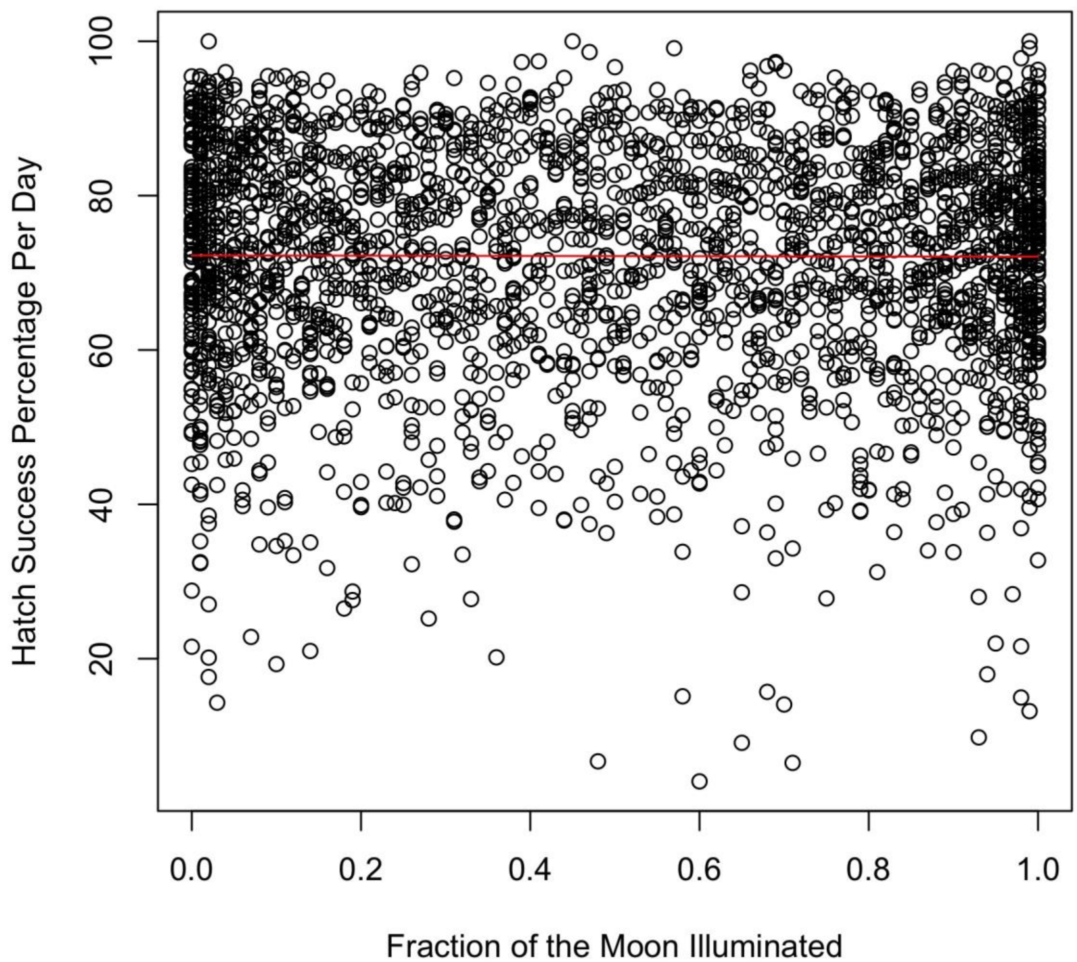


Figure 26). However including the squares of each variable and their interactions in the multiple regression model increased the explanation of variation to 30.7%. A summary of this regression model can be seen in **Table 5** of the Appendix.

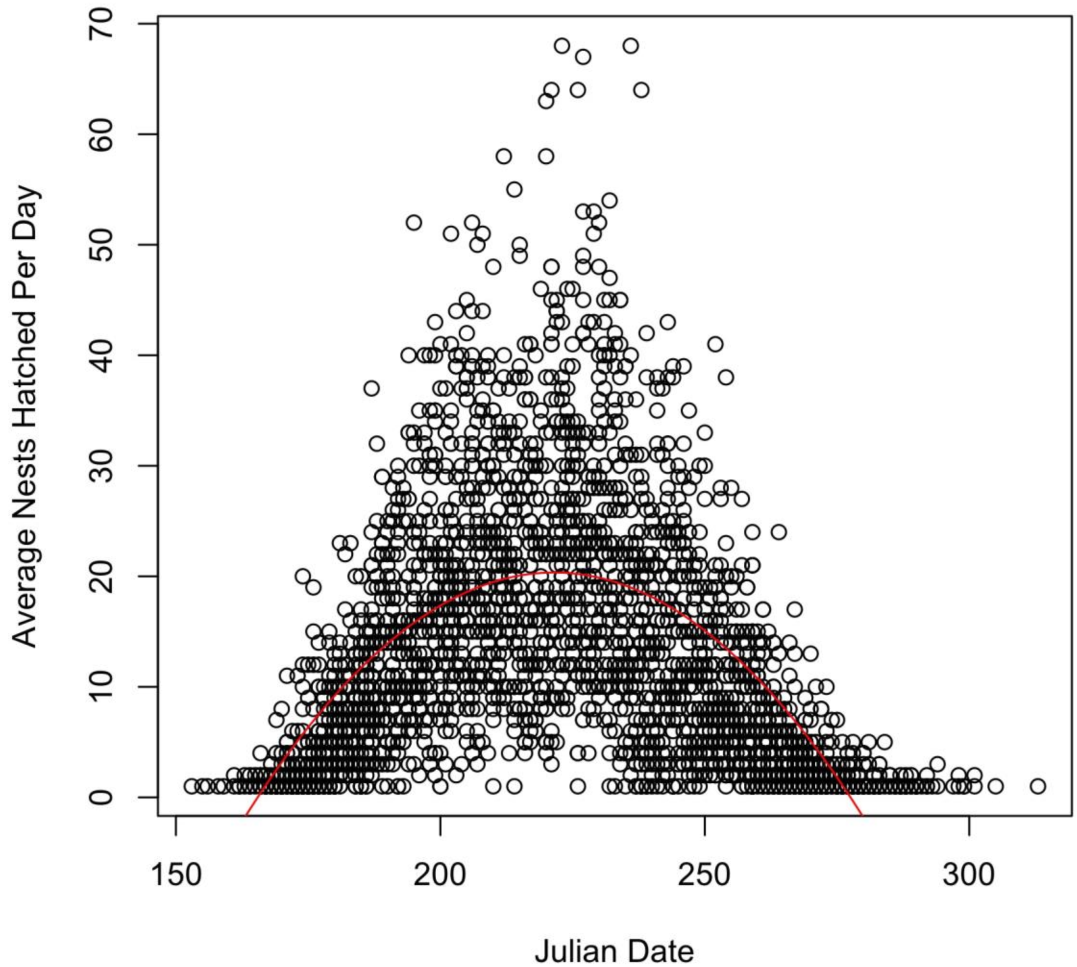


Figure 5: Average number of loggerhead nests hatched compared to Julian date from 1991-2015. Polynomial model: $y = -0.006X^2 + 2.869X – 297.4$, $R^2 = 0.339$, $p < 0.001$

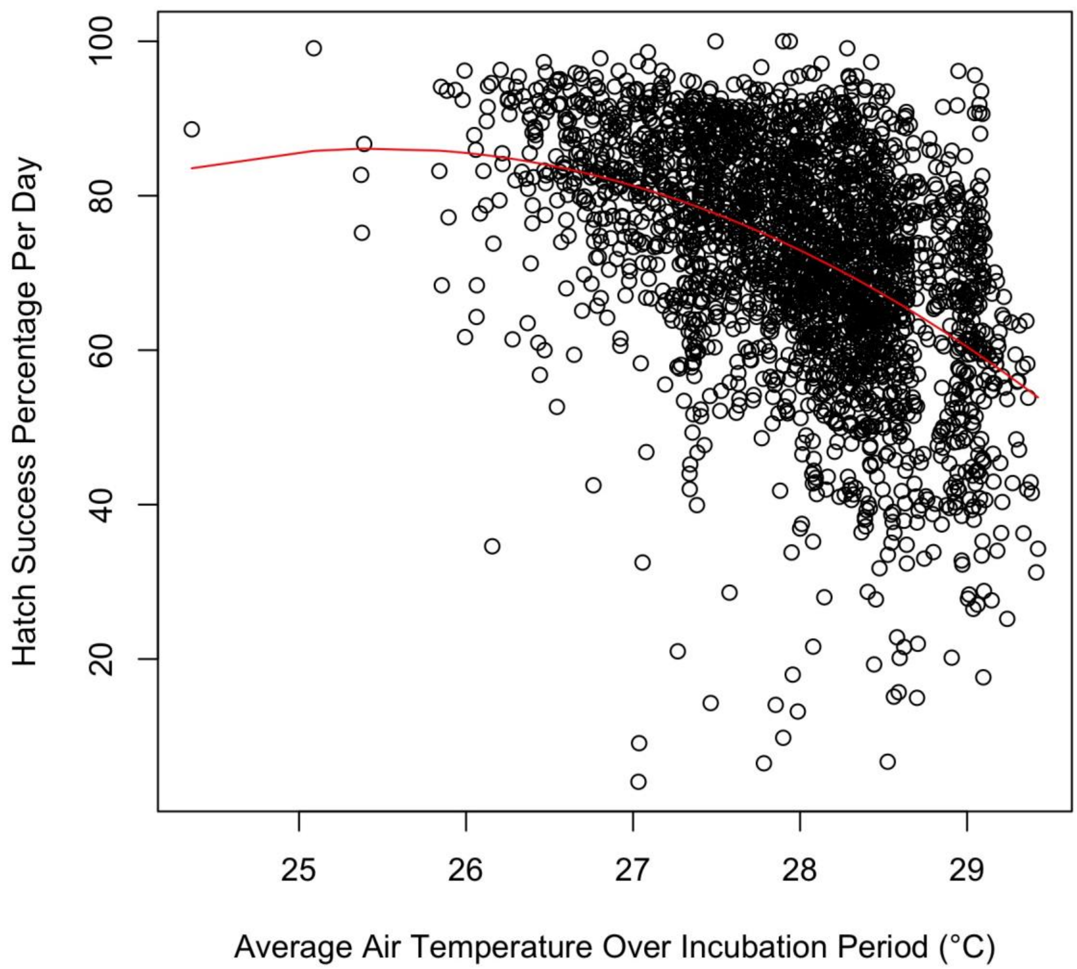


Figure 6: Hatch success percentage compared to average air temperature over the average incubation period (°C).
Polynomial model: $y = -2.063X^2 + 105.101X - 1{,}252.444$, $R^2 = 0.210$, $p < 0.001$

INCUBATION INTERVAL

Both lay dates and hatch dates for each individual nest had significant curvilinear relationships to the length of the incubation period (Appendix: **Figure 27 - Figure 28**). This relationship suggests longer incubation periods towards either end of the season and shorter incubation periods during the peak of the season. This was concurrent with the curvilinear relationships apparent between the average length of the incubation period and air temperature, sea surface temperature, and precipitation over the incubation period. Both air temperature and sea surface temperature had a negative relationship with the average length of the incubation period, with warmer temperatures resulting in shorter incubation periods (Figure 7 -

Figure 8). These models estimate a 1°C increase in air and sea surface temperatures would subtract 2.6 and 2.2 days from the incubation period respectively. However precipitation had a positive relationship with the average length of the incubation period, such that greater amounts of precipitation resulted in longer incubation periods (**Figure 9**). This model suggests that an increase of average precipitation by 1 centimeter per day would increase the length of the incubation period by 0.46 days. Hatch success percentage also had a weak relationship to the length of the incubation period, but the fitted regression suggested a slight increase in hatch success percentage with respect to longer incubation periods (Appendix:

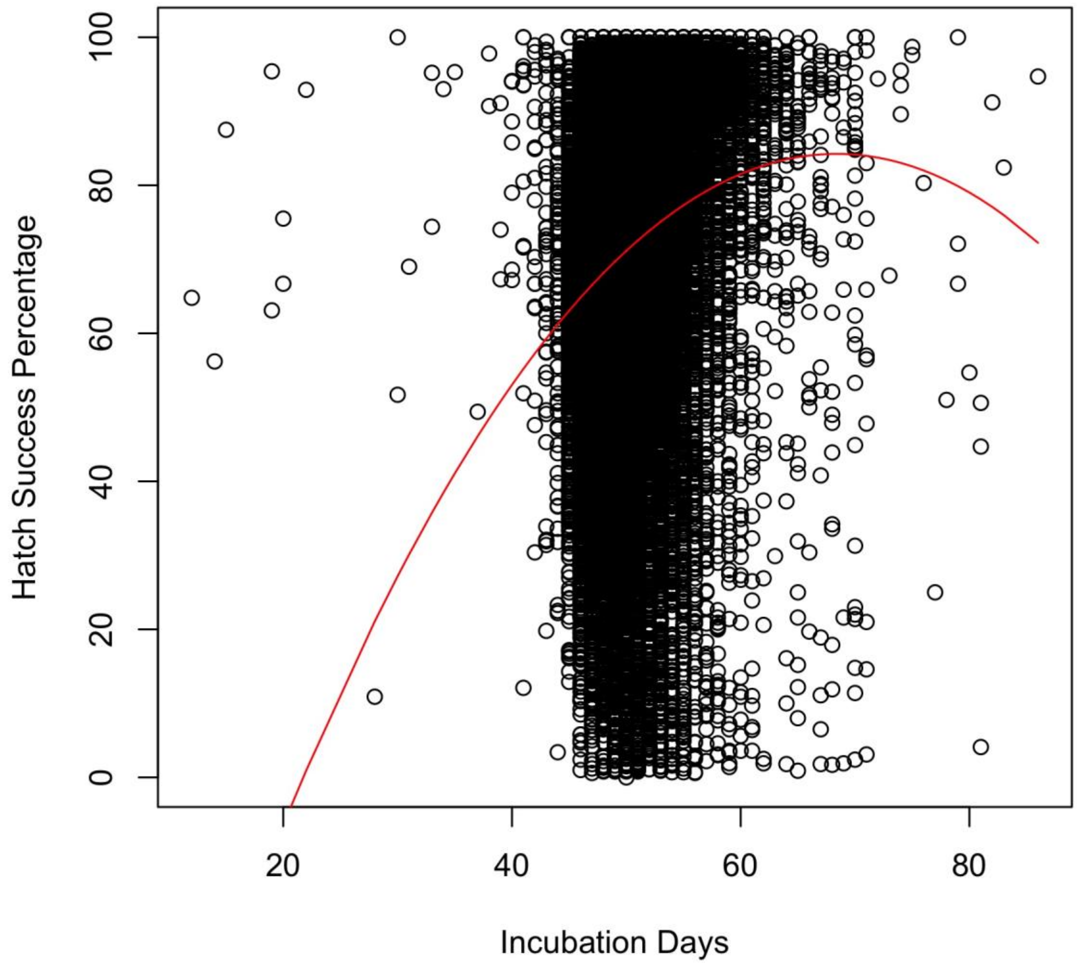
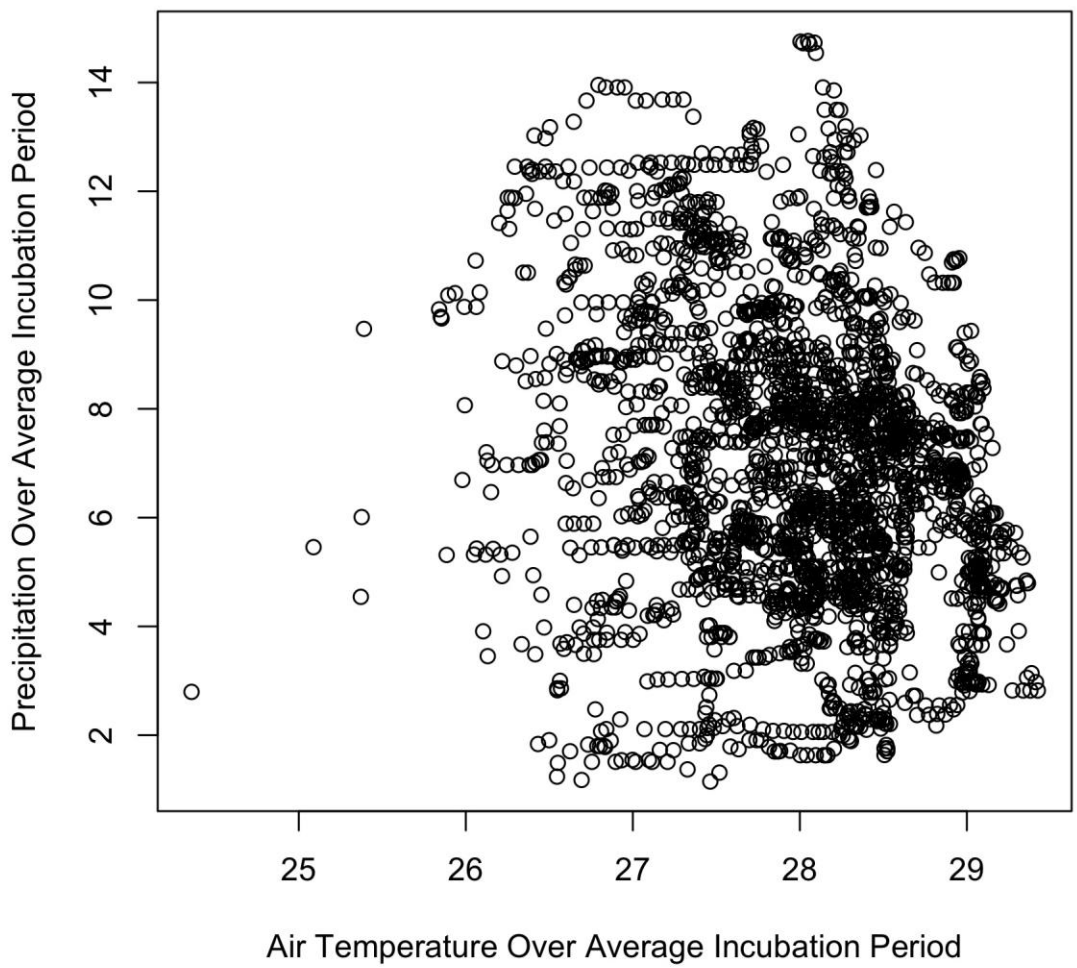


Figure 29). This suggests that warmer temperatures and decreased precipitation result in shorter incubation periods, which in turn results in decreased hatch success percentages. The correlations between sea surface temperature, air temperature, and precipitation over the average length of the incubation period can also be found in



Precipitation Over Average Incubation Period
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Air Temperature Over Average Incubation Period

Figure 30 -

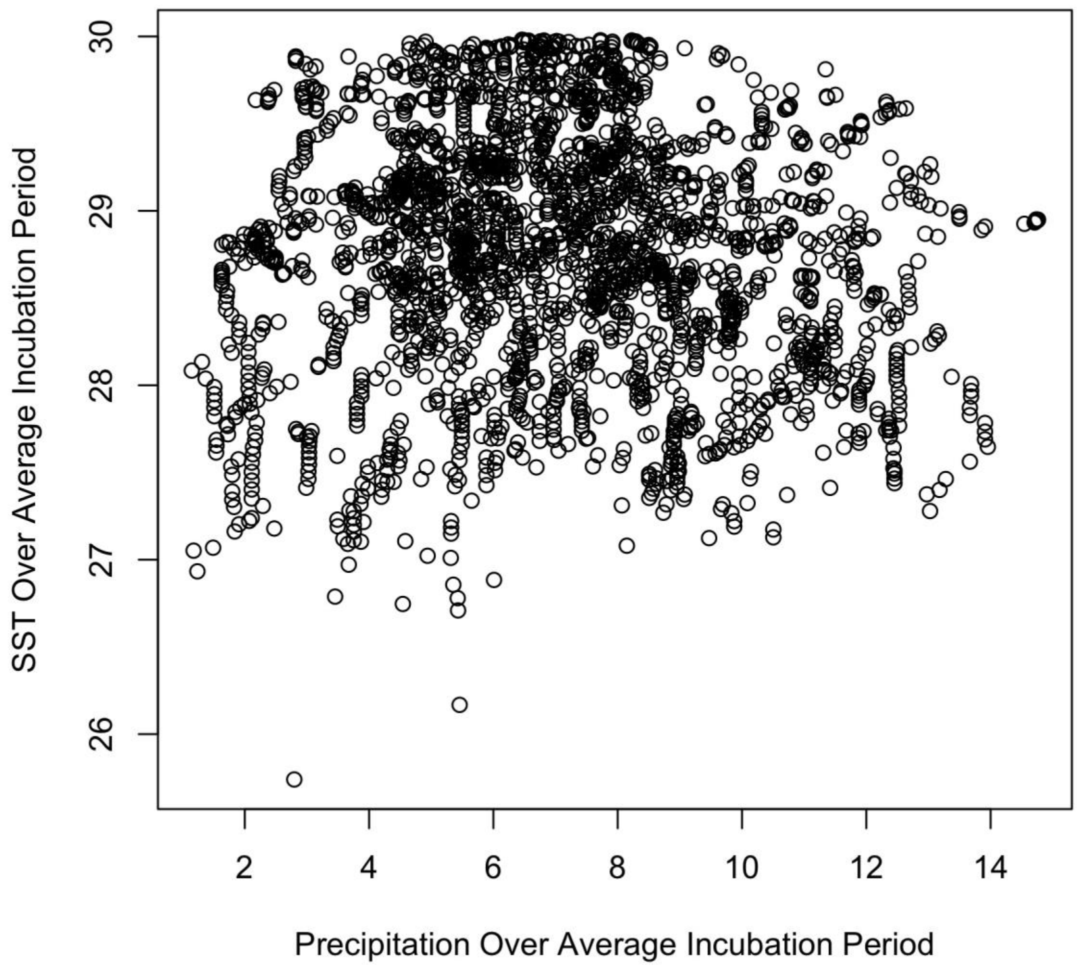

Figure 32 of the Appendix.

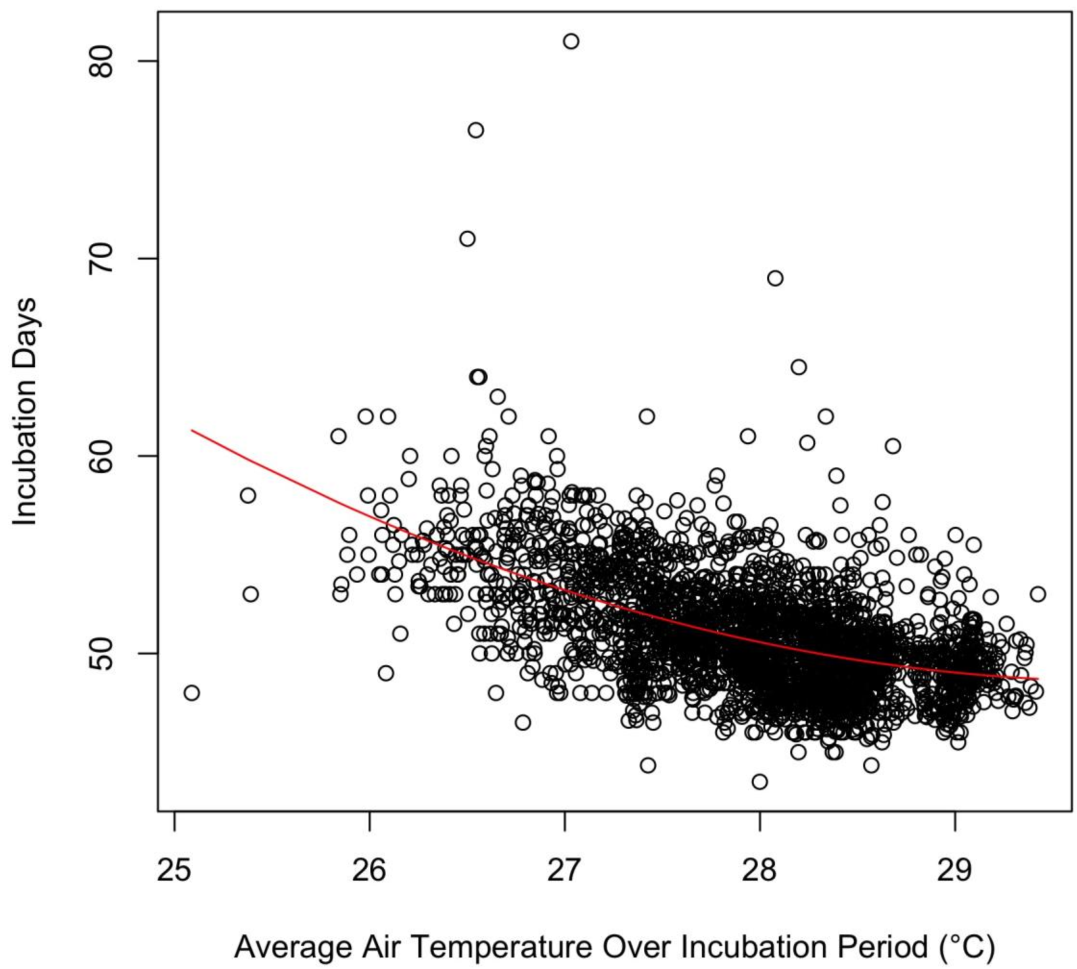

Figure 7: Average air temperature over the average incubation period (°C) compared to total length of the incubation period. Polynomial model: $y = 0.549X^2 - 32.819X + 539.239$, $R^2 = 0.299$, $p < 0.001$

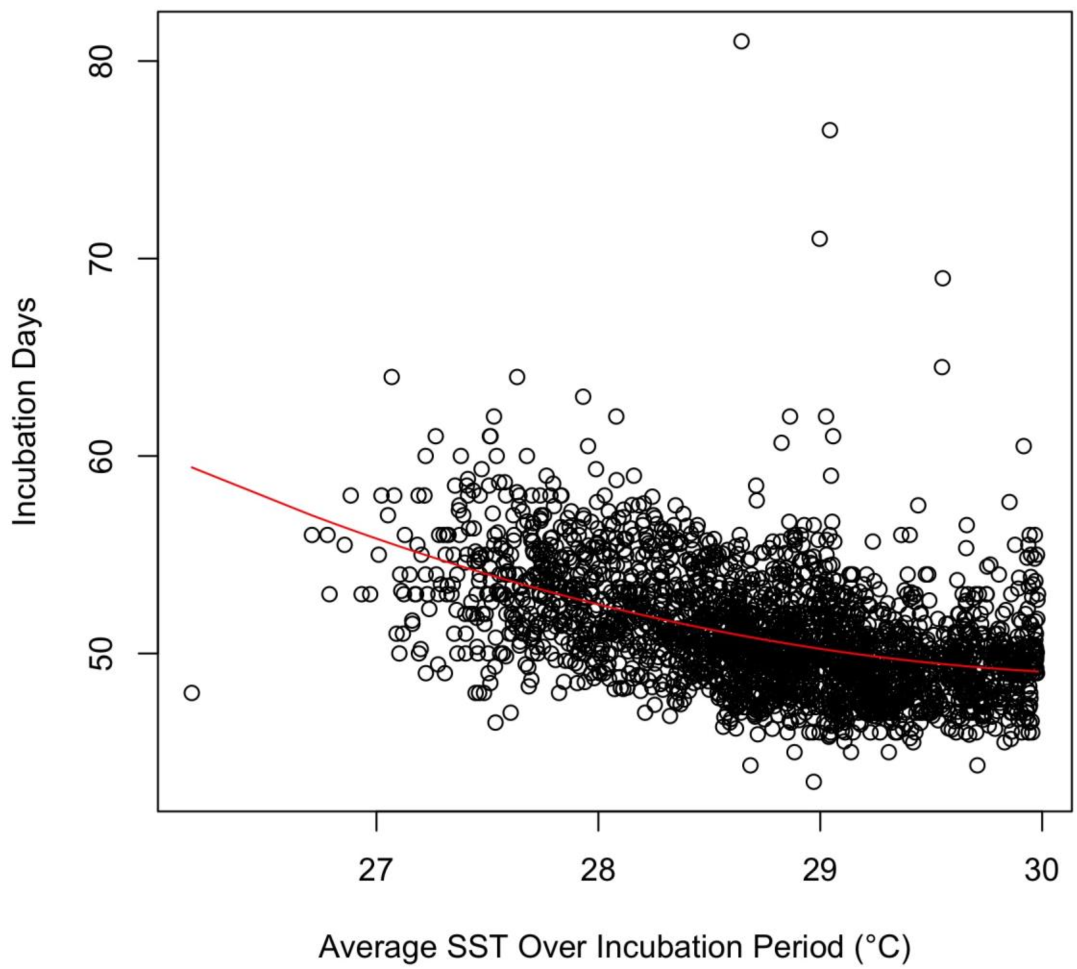

Figure 8: Average sea surface temperature over the average incubation period (°C) compared to total length of the incubation period.
Polynomial model: $y = 0.545X^2 - 33.294X + 557.667$, $R^2 = 0.236$, $p < 0.001$

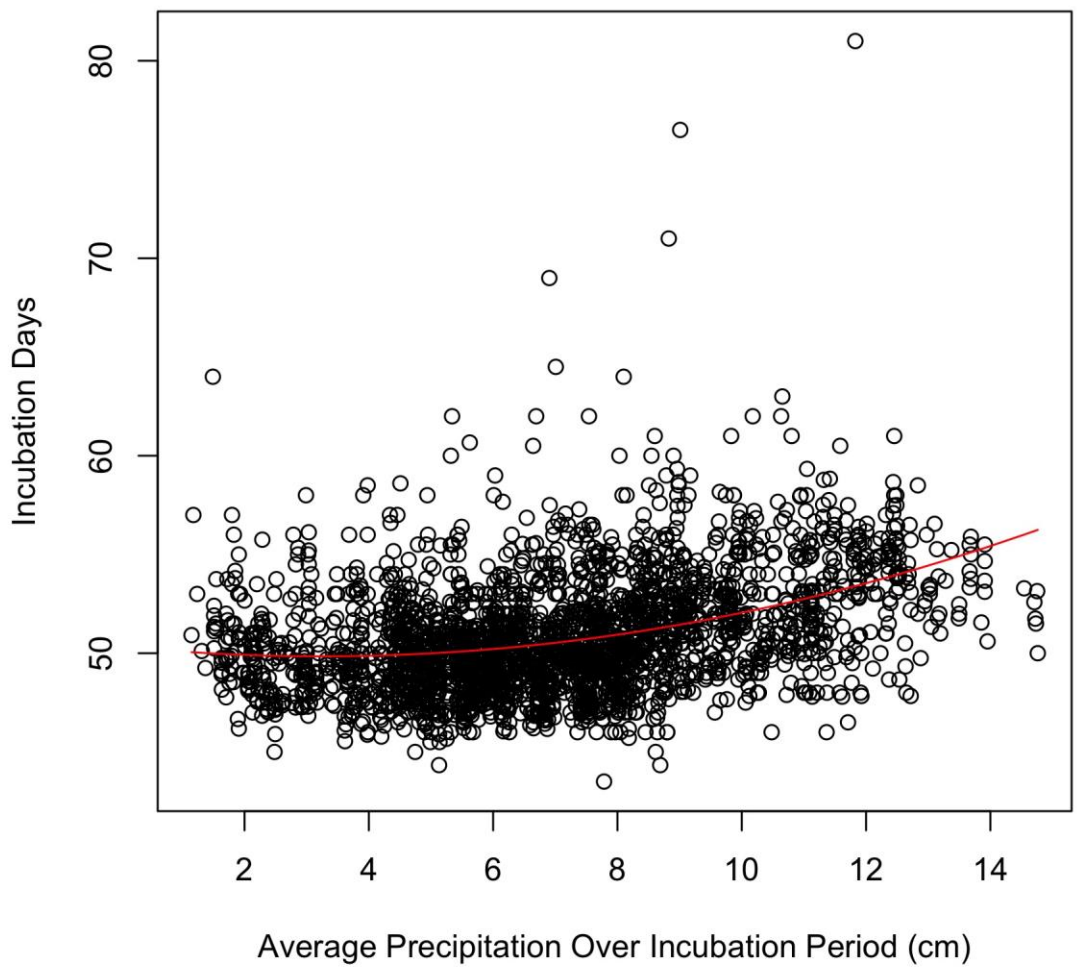

Figure 9: Average precipitation over the average incubation period (cm) compared to total length of the incubation period. Polynomial model: $y = 0.048X^2 – 0.311X + 50.245$, $R^2 = 0.147$, $p < 0.001$

Discussion

TEMPORAL TRENDS

Over the 25-year study period from 1991-2015, degrees of both consistency and fluctuation could be observed in the patterns of environmental variables and sea turtle nesting and hatching behavior. Each season had a very consistent parabolic trend, which explained the high standard deviation of nests laid, nests hatched, and false crawls per day. Occurrences of nesting and false crawls began slowly in the spring months, gradually increased towards the warmer summer months, and then gradually died down again towards the end of the season. The trend of the hatching season followed a similar pattern, albeit shifted towards later Julian dates. These seasonal trends occurred every year, regardless of other environmental factors.

From year to year the seasonal parabolic patterns remained predictable, but at first glance the other temporal patterns of nesting and hatching behaviors did not. None of the nesting or hatching variables (First emergence date, total number of nests per year, length of the nesting season, etc.) demonstrated clear directional trends over time. Instead, many occurrences of these variables appeared random and scattered. However many of these seemingly random patterns shared similar shapes and magnitudes with corresponding patterns of environmental variables. This suggests that while these behaviors have not yet experienced any long-term or permanent shifts in Broward County, they do respond together in accord with the environmental fluctuations that occur from year to year.

This environmental responsiveness is not unexpected, nor is the lack of a dramatic phenological shift in Broward County. The climate conditions in subtropical South Florida have not experienced drastic directional changes over the 25-year study period, so it is logical that environmentally-dependent sea turtle nesting and hatching patterns would follow suit. Similar studies in Florida and Costa Rica also found a lack of identifiable phenological shifts due to local climate conditions, suggesting that climate changes in these areas have not yet had a lasting impact on local behaviors (Mazaris et al., 2008; Neeman et al., 2015; Pike, 2006; Weishampel et al., 2010). However the close ties between sea turtle behaviors and their surrounding environmental conditions suggests that future climate shifts may result in eventual parallel shifts in sea turtle phenology.

PREDICTIVE PARAMETERS

Nesting

It is no surprise that sea surface temperature was found to be the strongest indicator for sea turtle nesting numbers, as it is a known proxy for many sea turtle behaviors including foraging, migration, and nesting trends (Chaloupka et al., 2008; Girondot and Kaska, 2015; Pike et al., 2006; Pike, 2008; Pilcher et al., 2014). The female turtle is in direct contact with her pelagic oceanic habitat, making ocean temperatures (most easily measured as sea surface temperature) a logical primary cue for seasonal and other temperature-related behaviors. However it is interesting to note that the individual plot of nesting numbers with respect to sea surface temperature most closely resembles the plot of the same behavior with respect to Julian date. Not only this, but the R^2 value of the Julian date regression was over twice as high as the sea surface temperature regression. Therefore it is possible that nesting numbers are more strongly dependent on other seasonal or climate factors, which are merely exemplified by patterns in sea surface temperature. This study was not able to differentiate whether the nesting number alignment with sea surface temperature was causative or correlative, so further research would be necessary to determine whether females actively use ocean temperatures as a cue to lay their nests, or whether temperature is merely a proxy for another unknown seasonal cue.

However there is no denying sea surface temperature as a useful proxy for determining sea turtle nesting numbers. The individual regression model for sea surface temperature was able to explain 23.3% of the variation in sea turtle nesting numbers, which was not much less than the 26.2% explained by the multiple regression model including supplementary environmental variables, their squares, and their interactions. While the additional environmental variables could not be removed from the multiple regression while still maintaining a statistically similar R^2 value, it is clear that sea surface temperature explains the majority of the variations in nests laid. Both the individual regression model for sea surface temperature and the multiple regression model are capable of predicting seasonal nesting trends, but it could be argued via the principle of Occam's razor that the added complication to the multiple regression model is not justified by the small increase in the R^2 value. Therefore the individual polynomial regression model depicting sea surface temperature effects on sea turtle nests laid could be considered the most efficiently effective model for predicting seasonal nesting trends.

Hatching

While environmental factors are useful as proxies for predicting sea turtle nesting behaviors, these external factors can have an even more direct impact on hatching success. This is due to the increased susceptibility to and dependence on environmental conditions that developing embryos have compared to nesting females, and the powerful influence that environmental factors have on the nesting beach and resultant incubation conditions (Drake and Spotila, 2002; Pike, 2014). In this study air temperature over the incubation period served as the most important determinant of hatch success percentage, surpassing sea surface temperature over the incubation period and daily values of temperature and precipitation on the hatch date. Several sea turtle studies have supported these findings, as previous research has shown increasing air temperatures to affect emergence rates and hatching success due to the direct effect on nest temperatures and incubation conditions (Girondot and Kaska, 2015; Hays et al., 1999; Saba et al., 2012). Therefore air temperature over the incubation period is not only an expository for hatch success percentage, but also an environmental factor with a measurable causative relationship to loggerhead hatching events.

However in contrast with nests laid, the addition of supplementary environmental variables and their squares greatly increased the R^2 value of the multiple regression model. In this case, values of environmental variables over the incubation period were included in addition to daily values of these variables in order to give the best representation of the comprehensive conditions that each loggerhead nest experienced. Utilizing the averages of these variables over the incubation period was crucial for understanding the cumulative impacts on each nest throughout the incubation period, but could not indicate whether environmental events were evenly spread throughout the incubation period or if they were the average of mild and extreme conditions (Booth and Evans, 2011). Therefore incorporating daily values to account for local climate conditions on the hatch date allowed the multiple regression to tap into more of the potential environmental impacts that occurred prior to and during sea turtle hatching events. Including these additional manifestations of environmental variables increased the complexity of this model, but also greatly increased its predictive power. Therefore the multiple regression is the strongest model in this study for predicting hatch success percentage in Broward County.

Incubation

In addition to the effects on sea turtle nesting and hatching success, the environmental variables in this study also significantly affected the length of the incubation period. While the average length of the incubation period was rounded to 51 days, the actual length of the incubation period varied depending on the impacts of these environmental variables. The curvilinear regressions suggest that higher air and sea surface temperatures resulted in shorter incubation periods and increased precipitation resulted in longer incubation periods. These findings are in accord with those of several other environmental sea turtle studies. Considering air or sea surface temperature as a positively correlated proxy for beach temperatures, incubation period length is commonly found to have a negative relationship with nest temperatures for many species of reptile (Ackerman, 1997; Du and Shine, 2015; Hawkes et al., 2009; Matsuzawa et al., 2002; Reid et al., 2009).

The connection between these relationships also suggests that the healthiest hatchlings will occur earlier in the season when temperatures are cooler and incubation periods are longer. Warmer nest temperatures have been experimentally linked to decreased hatch success in reptiles, as higher temperatures increase metabolic rate, thereby reducing the length of the incubation period and the amount of yolk that is able to be converted to hatchling tissue (Booth and Evans, 2011; Mazaris et al., 2009). This increases the risk of congenital malformations in hatchlings, and can also result in reduced body size, reduced emergence rates, and increased embryonic mortality (Barcenas-Ibarra et al., 2015; Booth and Evans, 2011; Du and Shine, 2015; Reid et al., 2009; Saba et al., 2012; Weber et al., 2001). Considering that temperatures typically increase as the summer season progresses, it is fitting that hatch success percentages would decrease with the passage of time. Similar studies have shown as much as a 50% decline in hatching success from the first nests hatched in a season to the last (Broderick et al., 2000; Van Houtan and Bass, 2007; Saba et al., 2012). This reduced offspring viability ultimately results in decreased reproductive success, indicating that warming temperatures and decreased incubation periods could seriously affect sea turtle populations.

INTERACTION IMPORTANCE

Unfortunately the interactions between environmental variables can also have complex impacts on sea turtle nests, often making them more difficult to interpret. For example, the combined R^2 values for each individual environmental variable affecting hatch success percentage add up to 43.90, while the multiple regression model encompassing these same variables only has an R^2 value of 30.7. The total amount of variance explained by each individual environmental variable notably outweighs the amount of variance explained by the multiple regression model including important interactions. This disparity between hatch success percentage models is most likely due to the strong correlation between air temperature and sea surface temperature over the incubation period, such that air and sea surface temperatures are both accounting for the same variation in hatch success percentage (Pike, 2008; Weishampel et al., 2004). One study by Girondot and Kaska (2015) suggests that sea surface temperature is actually a better predictor for nest temperatures and hatch success percentage than air temperature, but the strong correlation appears to enhance the effects of air temperature on sea turtle nests.

It is also possible that the interactions between variables in this study could have confounding effects on one another (Girondot and Kaska, 2015). While the negative correlations between precipitation, air temperature, and sea surface temperature over the incubation period were mild, it is still possible that increased precipitation could have counteracted the impacts of increased air or sea surface temperatures to varying degrees. Research by Lolavar and Wyneken (2015) suggests that increased precipitation can result in cooler nest temperatures, and the extent of the general cooling effect of rainfall is dependent on the depth of the nest. The abundance of rainfall also significantly affects how deep it will penetrate and to what extent it will affect sand temperatures and nest conditions, regardless of the surrounding air temperature (Lolavar and Wyneken, 2015). Therefore simple correlations may not be sufficient in capturing the complicated relationship between precipitation, air temperatures, and nest sand temperatures. Further research would be useful for picking apart these interactions between environmental variables and determining how their joint impact may influence sea turtles.

CLIMATE CHANGE CONCERNS

Environmental responsiveness is an evident component of sea turtle life history, but one that can quickly become deleterious in the context of climate change. Rising temperatures and environmental instability can have dramatic impacts on offspring viability, resulting in a significant decrease in overall reproductive success (Anderson et al., 2013; Reid et al., 2009; Saba et al., 2012; Weber et al., 2001). Considering the importance of the nest microclimate for proper development, increasing temperatures in particular could result in increased embryo mortality and decreased hatching success (Matsuzawa et al., 2002; Saba et al., 2012). The inter-seasonal variation demonstrated in this study depicts how increased temperatures can negatively affect sea turtle hatching rates, and the dramatic increases created by climate change could push many new loggerhead nests past their temperature tolerances (Walther et al., 2002). Permanently increased temperatures could shift loggerhead hatching success rates to the lower percentages of its range, resulting in permanently decreased reproductive success.

As climate change progresses and temperatures continue to rise, sea turtle survival will depend upon their ability to avoid these repercussions or acclimate to changing conditions. Previous studies have shown that species that fail to respond to environmental changes have decreased greatly in abundance over time (Willis et al., 2008). While the cues for gravid females to nest are complex and mysterious, it is possible that nesting females could be able to respond to warming trends by shifting the phenology of their nesting events earlier towards cooler parts of the year (Chaloupka et al., 2008). If the need for avoiding warmer temperatures overcomes the innate instinct to return directly to their natal beach, gravid females could also shift their nest locations towards higher latitudes and cooler beaches (Chaloupka et al., 2008; Perry et al., 2005). Understanding how loggerhead sea turtles are able to respond to climatic cues is therefore crucial when considering the potential consequences of climate change. Whether loggerhead females are able to make these phenological shifts will determine the levels of reproductive stress that they will experience in coming years, and their chances of survival in the long-term (Bradley et al., 1999; Cheng et al., 2013).

Conclusions

The nesting behavior of loggerhead females over 25 years in Broward County Florida provides notable insight into sea turtle life history patterns. Overall, the models produced in this study account for the most prominent environmental variables known to affect sea turtle behaviors. The graphical depictions of nesting season patterns from 1991-2015 demonstrate the fluctuations that have occurred over 25 years, and the regression models explain how environmental variables can impact these patterns. These models not only depict the patterns of nesting, incubation, and hatching, but can also predict future reproductive success and response to climate change. The best predictive models for sea turtle nesting and hatching behaviors stem from combinations of sea surface temperature and air temperature, suggesting that these variables are crucial for considering how sea turtles will respond to their environment, and reinforcing the idea that sea turtles are extremely temperature-dependent in many ways. Future research could utilize additional environmental variables to explain an even larger percentage of the variation in sea turtle patterns, and could delve deeper into the intricate relationships between variables and their influence on one another.

From these models, the Broward County Sea Turtle Conservation Program could use environmental projections to predict the outcomes of the nesting and hatching seasons. This would allow the program to predict its needs for monitoring effort, and to have a projected expectation of yearly nesting and hatching numbers. From these data it could be possible to estimate sex ratios, measure population stability, and establish quantitative population trends (Chaloupka, 2001; Hawkes et al., 2009). These results could even be extrapolated to help determine which management strategies could protect or enhance the sustainability of sea turtle nesting habitats in all of South Florida. Increasing our understanding of how and to what extent sea turtles respond to climate variables will lead to stronger support for conservation measures to mitigate climatic impacts, and will help us to protect sea turtle populations both locally and globally.

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Appendix

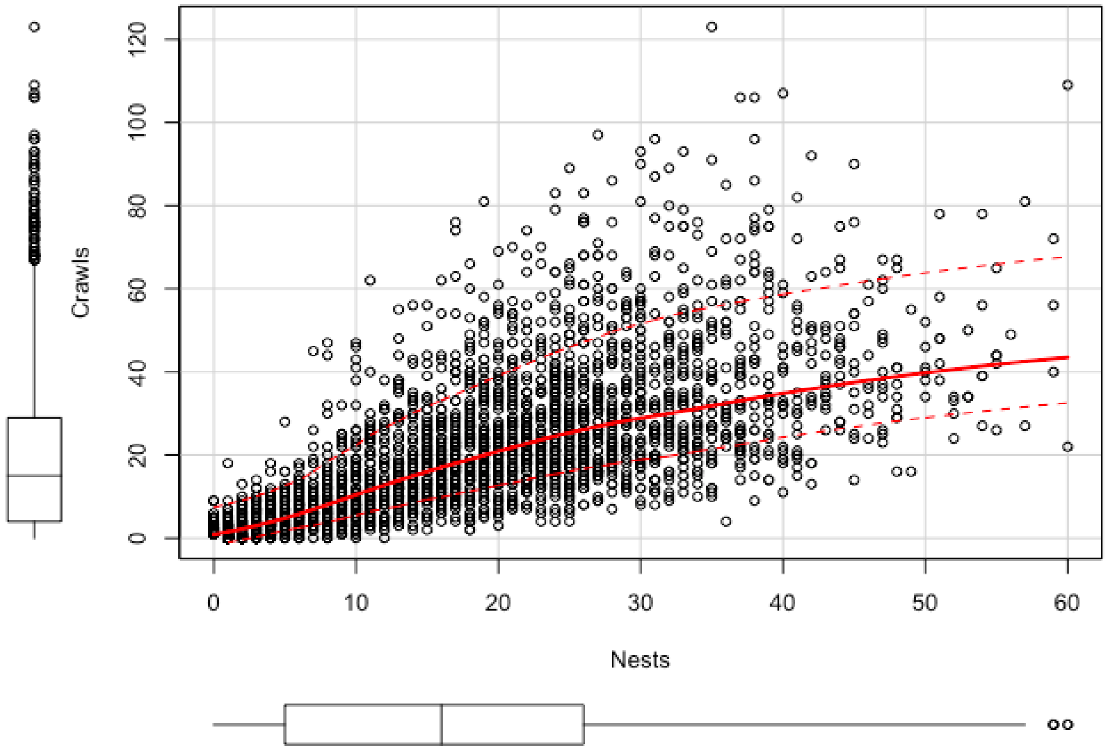

Figure 10: The number of successful loggerhead sea turtle nests laid compared to the number of false crawls on a given day. Correlation: p < 0.001, tau = 0.6442407

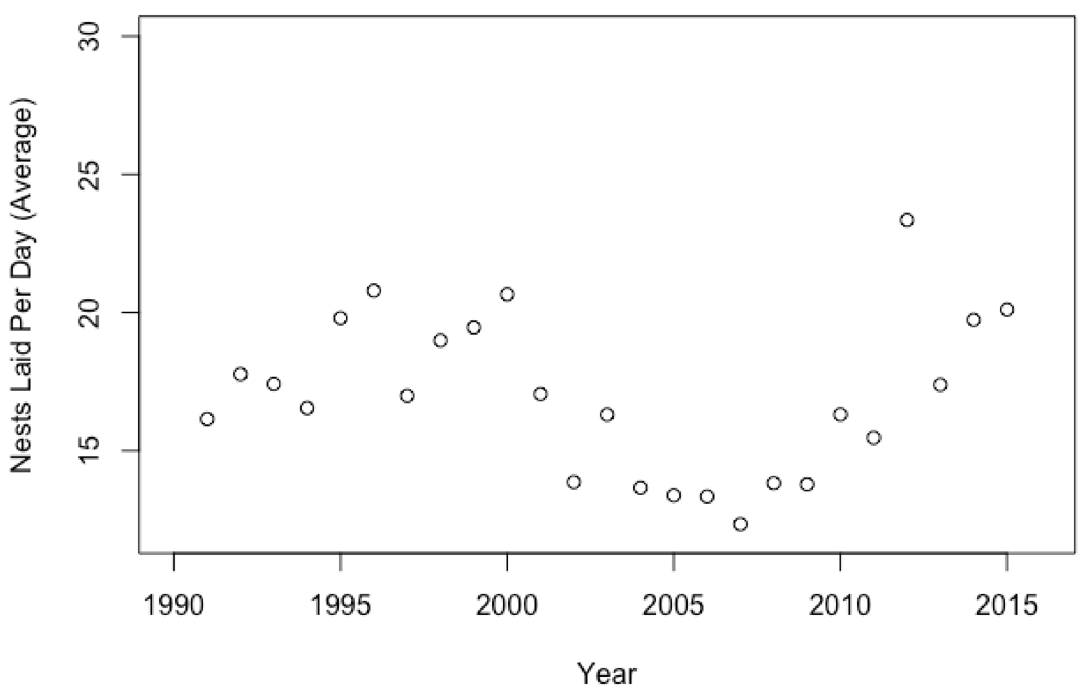

Figure 11: The average number of loggerhead sea turtle nests laid per day from 1991-2015

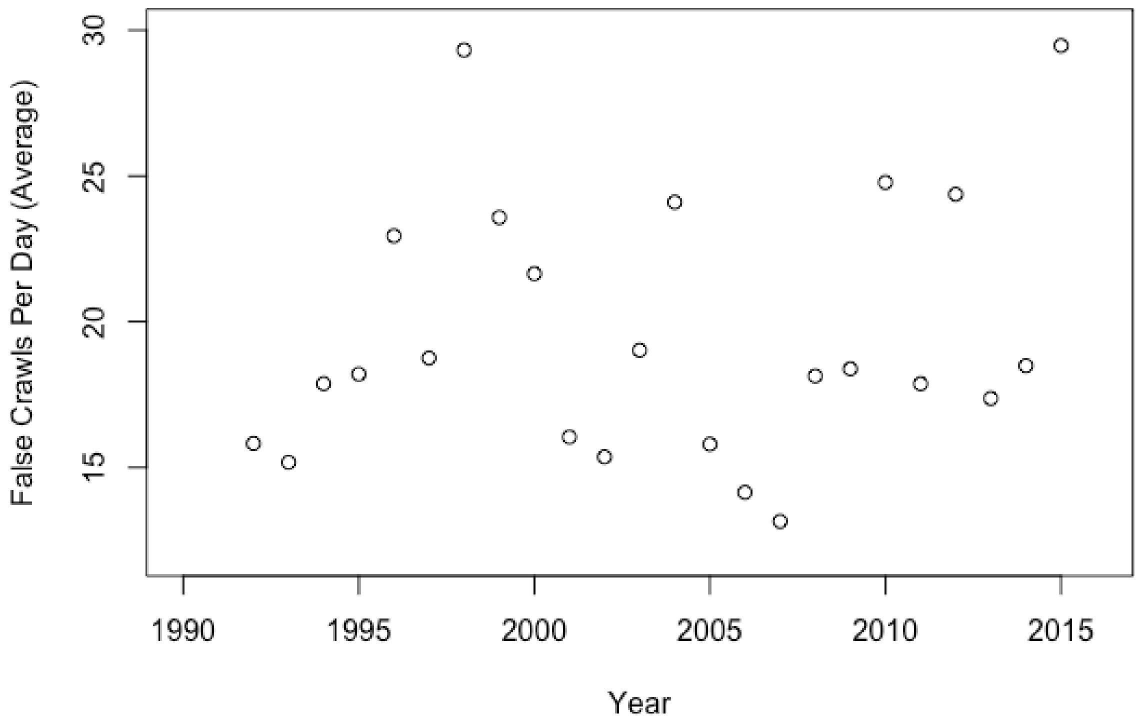

Figure 12: The average number of loggerhead sea turtle false crawls per day from 1992-2015

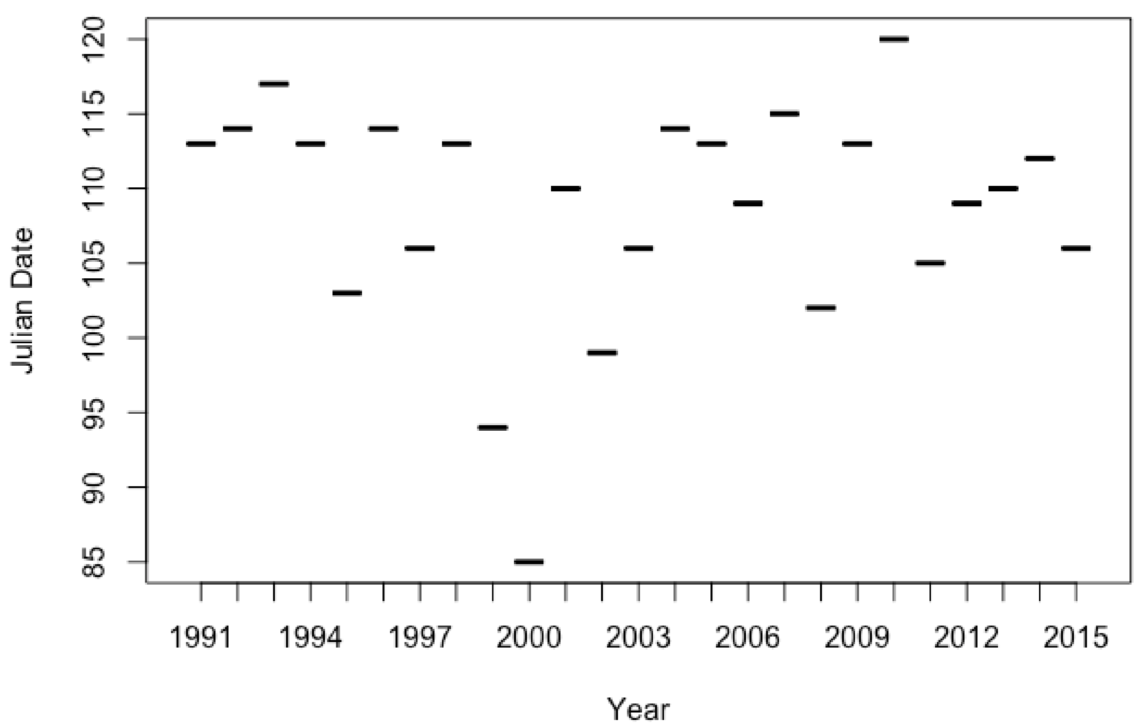

Figure 13: The Julian dates of the first loggerhead sea turtle emergences from 1991-2015

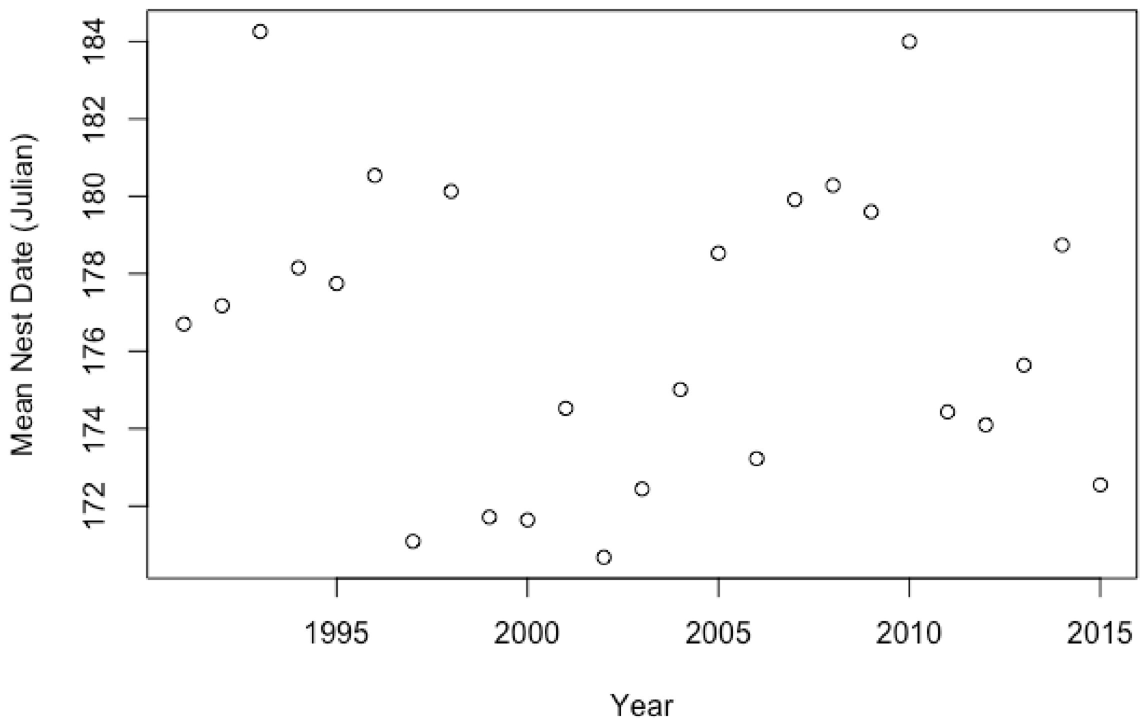

Figure 14: The mean loggerhead sea turtle nesting dates from 1991-2015

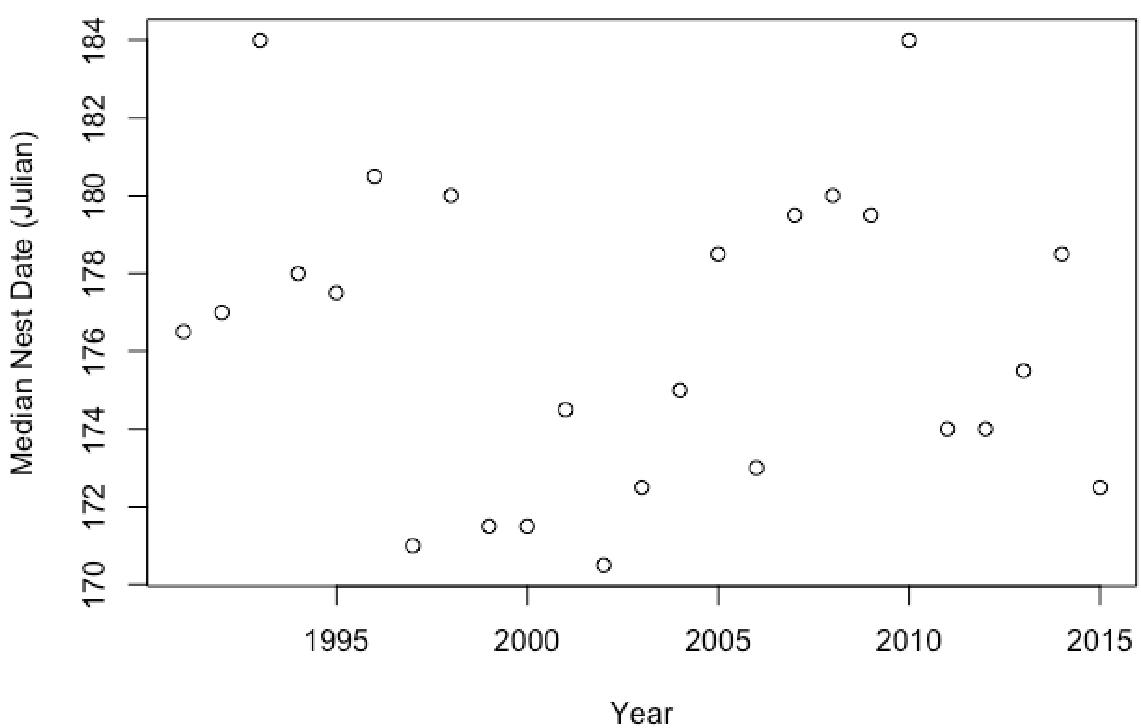

Figure 15: The median loggerhead sea turtle nesting dates from 1991-2015

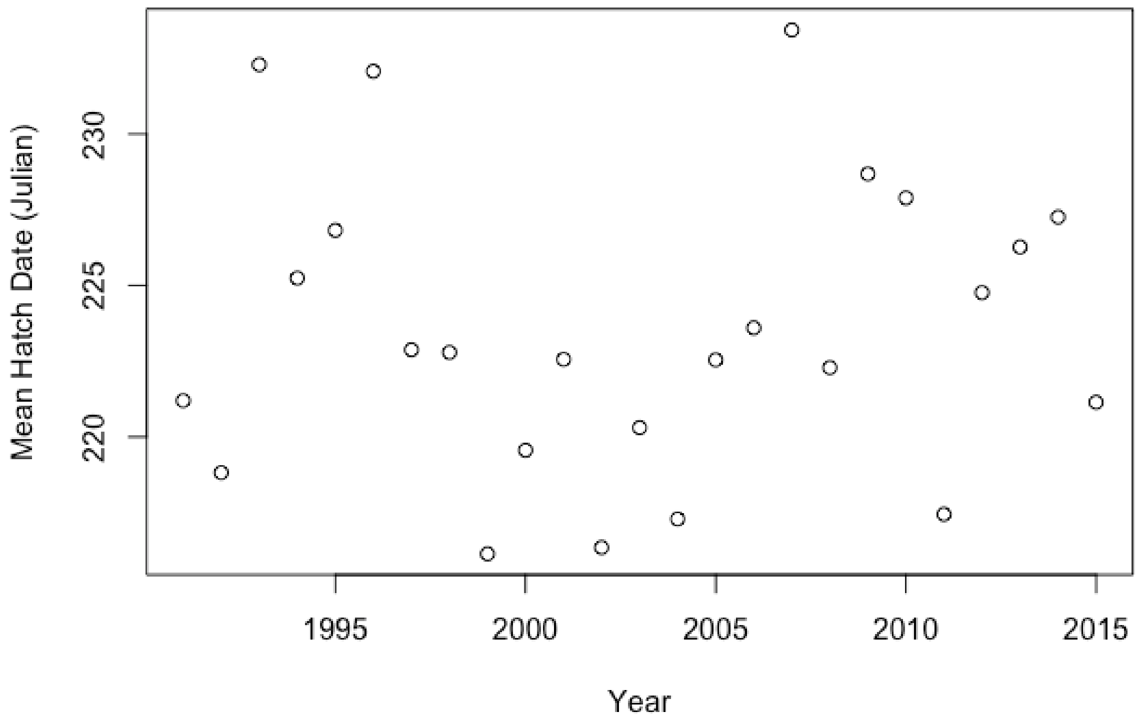

Figure 16: The mean loggerhead sea turtle hatching dates from 1991-2015

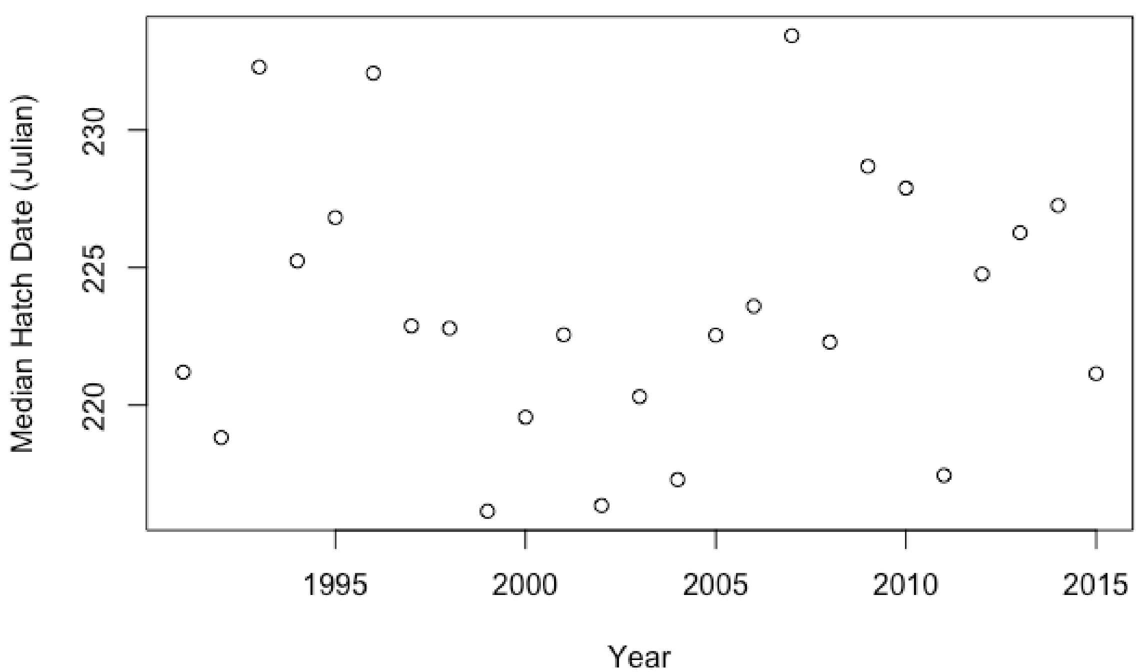

Figure 17: The median loggerhead sea turtle hatching dates from 1991-2015

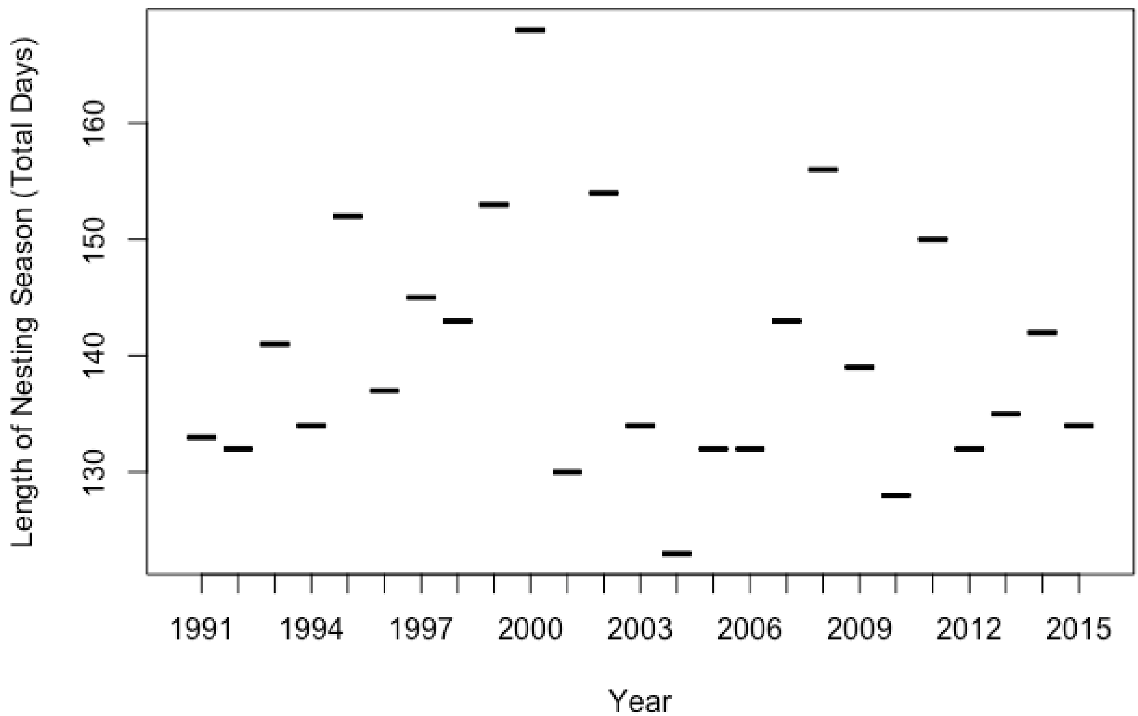

Figure 18: Lengths of the loggerhead sea turtle nesting season from 1991-2015. The average nesting season length over this 25-year period was 140 days.

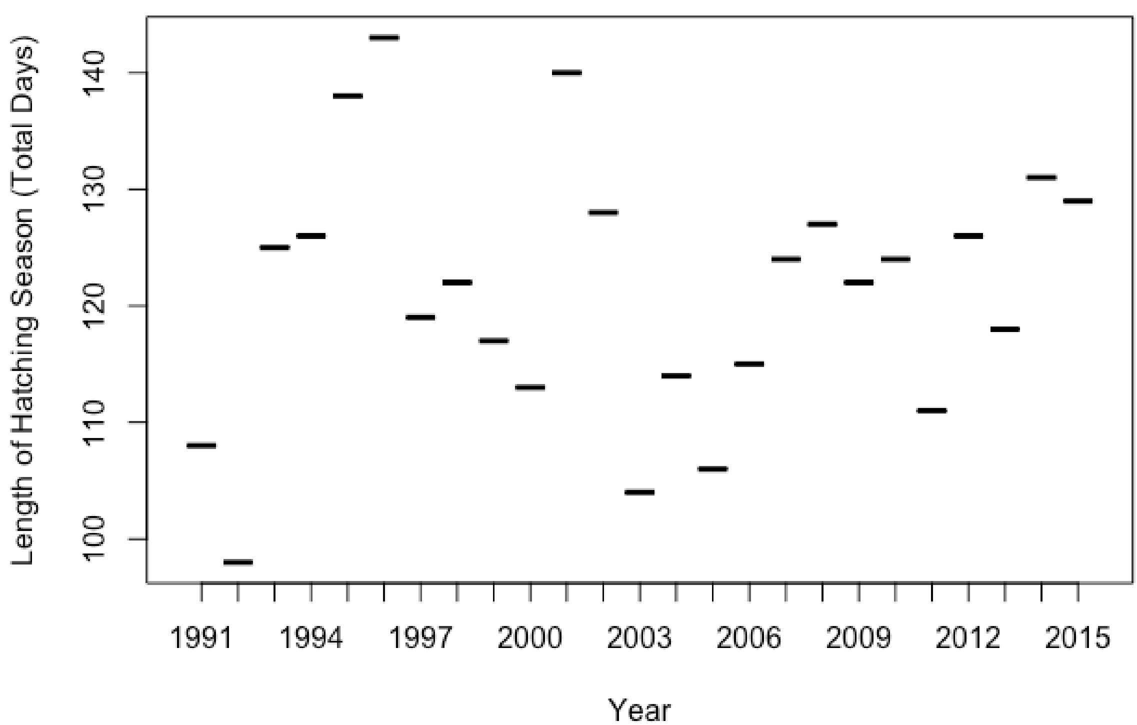

Figure 19: Lengths of the loggerhead sea turtle hatching season from 1991-2015. The average hatching season length over this 25-year period was 121 days.

Table 2: Summary table of loggerhead sea turtle nesting variables from 1991-2015

Year	Average number of nests laid per day	Total number of nests laid per season	Average number of false crawls per day	Total number of false crawls per season	Date of first emergence (Julian)	Mean nesting date (Julian)	Median nesting date (Julian)	Nesting season length (Total days)
1991	16.15	2002	NA	NA	113	176.70	176.5	133
1992	17.77	2221	15.82	1978	114	177.18	177	132
1993	17.41	2142	15.18	1867	117	184.26	184	141
1994	16.54	2134	17.88	2306	113	178.16	178	134
1995	19.80	2534	18.20	2330	103	177.75	177.5	152
1996	20.79	2661	22.95	2937	114	180.54	180.5	137
1997	16.98	2157	18.76	2382	106	171.09	171	145
1998	18.99	2336	29.32	3606	113	180.13	180	143
1999	19.46	2491	25.58	3018	94	171.71	171.5	153
2000	20.66	2644	21.65	2771	85	171.64	171.5	168
2001	17.05	2114	16.05	1990	110	174.52	174.5	130
2002	13.86	1830	15.36	2028	99	170.67	170.5	154
2003	16.30	2087	19.02	2435	106	172.44	172.5	134
2004	13.66	1625	24.10	2868	114	175.01	175	123
2005	13.38	1659	15.80	1959	113	178.53	178.5	132
2006	13.34	1614	14.15	1712	109	173.22	173	132
2007	12.34	1579	13.16	1684	115	179.91	179.5	143
2008	13.82	1894	18.14	2485	102	180.28	180	156
2009	13.78	1764	18.39	2353	113	179.60	179.5	139
2010	16.31	2006	24.78	3048	120	184.00	184	128
2011	15.47	2088	17.87	2413	105	174.43	174	150
2012	23.35	2965	24.37	3095	109	174.09	174	132
2013	17.38	2260	17.37	2258	110	175.64	175.5	135
2014	19.73	2605	18.49	2441	112	178.74	178.5	142
2015	20.11	2574	29.47	3772	106	172.55	172.5	134

Table 3: Summary table of loggerhead sea turtle hatching variables from 1991-2015

Year	Average number of nests hatched per day	Total number of nests hatched per season	Mean hatching date (Julian)	Median hatching date (Julian)	Hatching season length (Total days)	Average incubation period (Total days)	Average hatch success
1991	18.10	1828	221.20	221	108	49.43	65.04%
1992	15.77	1309	218.82	218	98	52.42	71.34%
1993	15.81	1692	232.29	232	125	48.82	64.52%
1994	14.50	1755	225.82	225	126	49.66	65.06%
1995	16.29	1890	226.82	226.5	138	51.26	73.64%
1996	15.42	1727	232.07	231.5	143	49.42	70.67%
1997	13.93	1463	222.88	223	119	49.25	70.56%
1998	14.96	1496	222.79	222.5	122	47.89	53.41%
1999	15.43	1327	216.14	215.5	117	51.82	64.87%
2000	12.91	1317	219.56	219.5	113	48.33	66.76%
2001	14.05	1461	222.56	221.5	140	50.86	68.87%
2002	11.67	1249	216.35	218	128	52.27	63.23%
2003	13.78	1364	220.30	220	104	49.56	68.78%
2004	11.34	941	217.29	216	114	49.55	61.24%
2005	13.22	1124	222.54	221	106	50.92	57.03%
2006	9.57	995	223.60	223.5	115	50.38	81.35%
2007	10.26	975	233.43	233	124	51.65	79.24%
2008	8.44	852	222.29	222	127	51.22	84.73%
2009	11.23	1089	228.69	228	122	51.47	74.90%
2010	12.57	1232	227.89	227.5	124	50.22	58.04%
2011	11.26	1194	217.44	217.5	111	50.68	78.60%
2012	17.52	1840	224.76	224	126	52.39	84.19%
2013	16.53	1802	226.27	226	118	52.96	88.29%
2014	16.85	1904	227.26	227	131	51.89	83.72%
2015	15.17	1699	221.14	220.5	129	49.72	73.79%

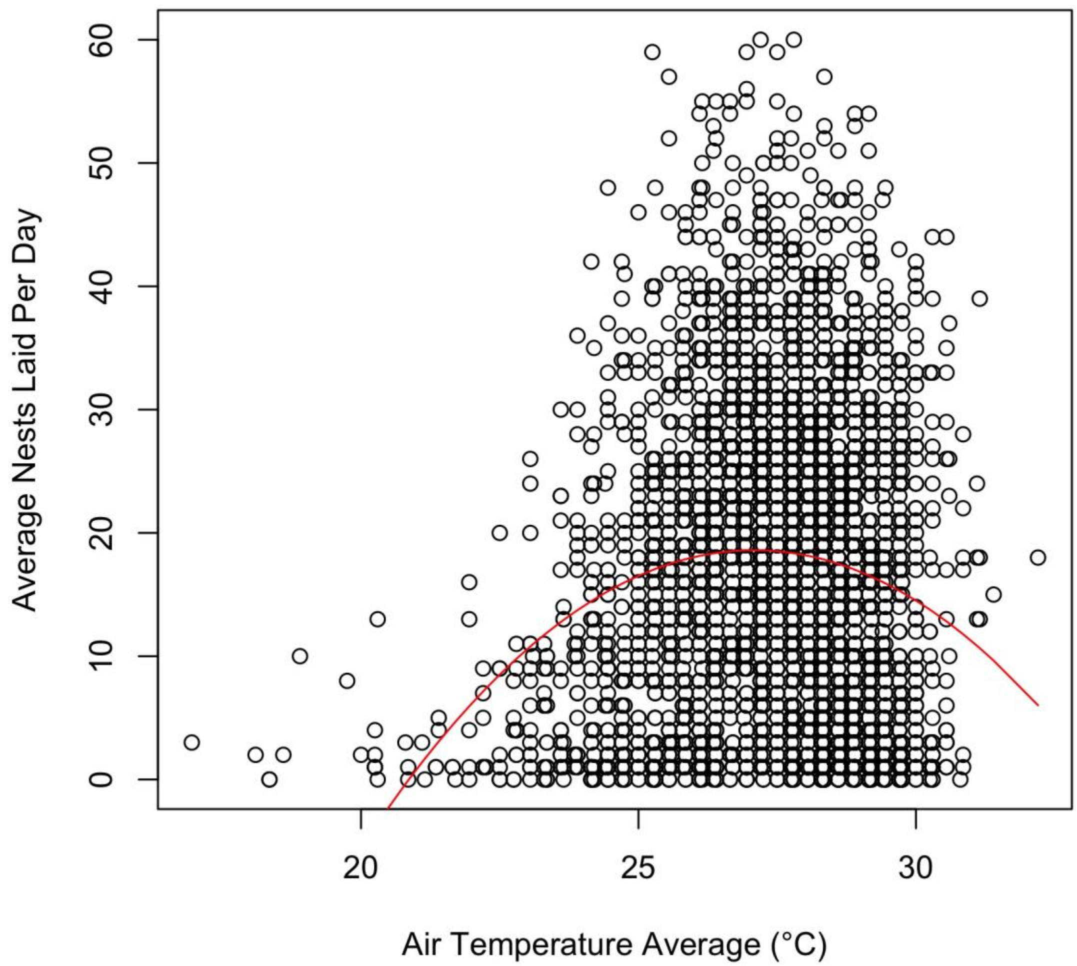

Figure 20: Average loggerhead nests laid per day compared to daily average air temperature (°C). Polynomial model: $y = -0.480X^2 + 26.025X - 333.815$, $R^2 = 0.047$, $p < 0.001$

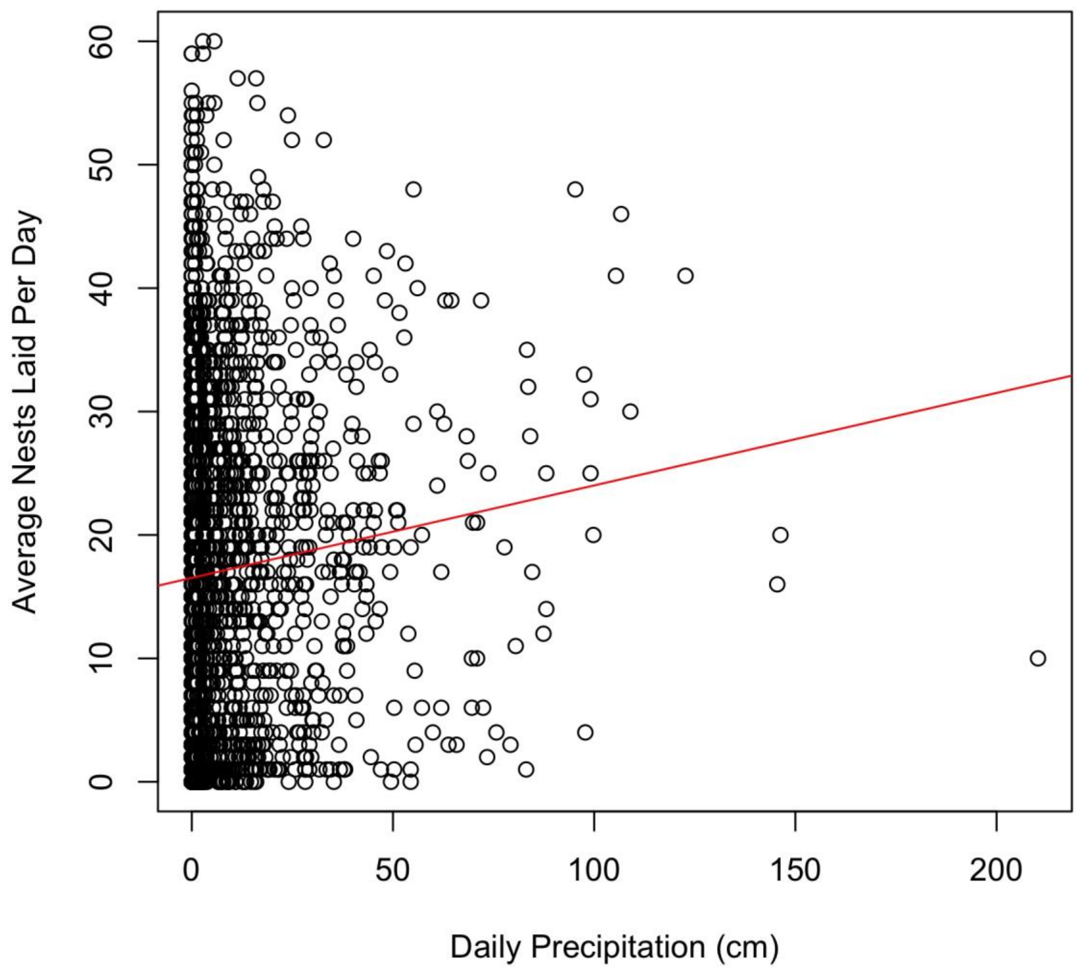

Figure 21: Average loggerhead nests laid per day compared to daily precipitation (cm). Linear model: $y = 0.0749X + 16.521$, $R^2 = 0.00661$, $p < 0.001$

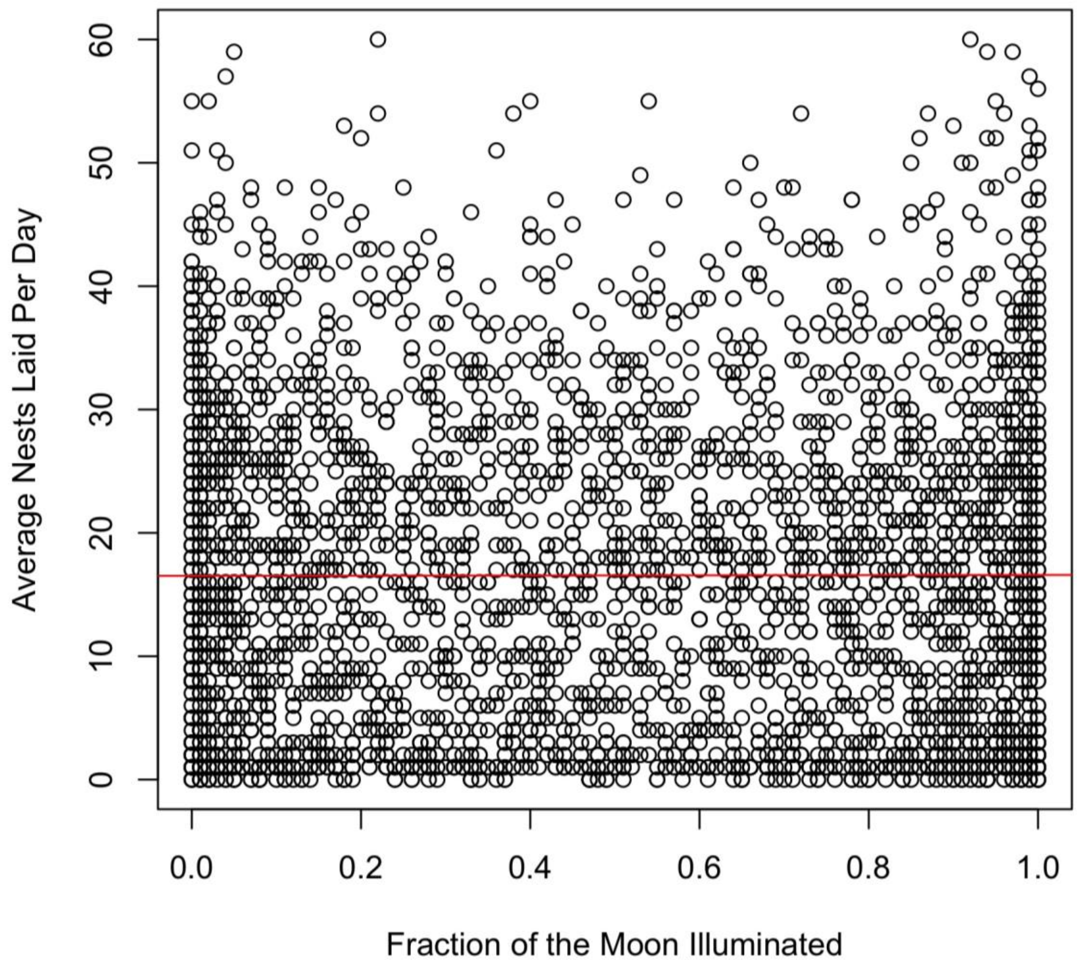

Figure 22: Average loggerhead nests laid per day compared to lunar fraction. Linear model: $y = -0.258X + 17.111$, $R^2 = 0.0000491$, $p = 0.693$

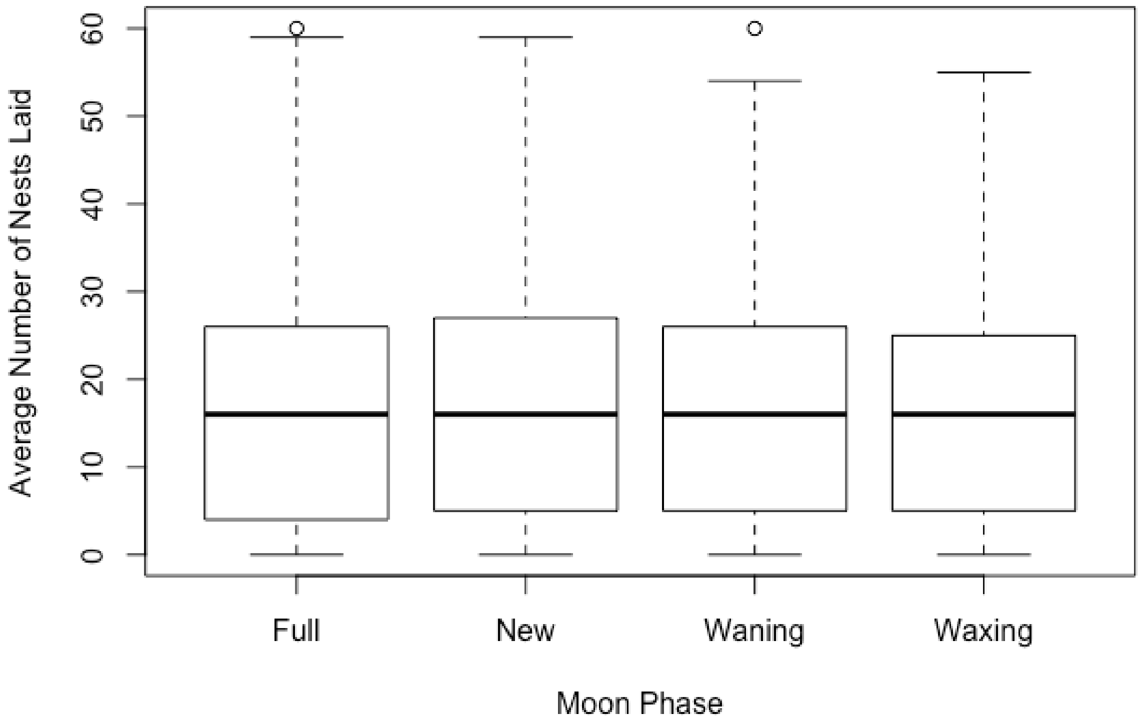

Figure 23: Average number of loggerhead nests laid per day compared to lunar phase. Kruskal-Wallis X^2 = 0.693, p = 0.875

Table 4: Coefficients for the most parsimonious polynomial regression model describing loggerhead sea turtle nesting numbers with respect to daily air temperature, sea surface temperature, precipitation, lunar fraction, and their interactions. Asterisks indicate the level of statistical significance.
$R^2 = 0.262$, $p < 0.001$

Coefficients	**Estimate**	**Std. Error**	**T Value**	**P Value**
Intercept	94,360	12,440	7.587	p < 0.001***
Lunar Fraction	-137.1	6.620	-2.071	p = 0.0384*
Air Temperature	-6,793	916.6	-7.411	p < 0.001***
I (Air Temperature^2)	118.1	16.94	6.972	p < 0.001***
Precipitation	1.145	0.421	2.717	p = 0.00663**
SST	-7,014	915.0	-7.665	p < 0.001***
I (SST$^{2)}$	130.0	16.82	7.728	p < 0.001***
Lunar Fraction : I (Precipitation$^{2)}$	-0.00149	0.000469	-2.453	p = 0.0142*
Lunar Fraction : I (SST^2)	0.0168	0.00824	2.038	p = 0.0416*
Air Temperature : SST	504.7	67.24	7.506	p < 0.001***
Air Temperature : I (SST^2)	-9.346	1.232	-7.585	p < 0.001***
I (Air Temperature^2) : SST	-8.784	1.239	-7.090	p < 0.001***
I (Air Temperature^2) : I (SST^2)	0.168	0.0263	7.192	p < 0.001***
Precipitation : SST	-0.0386	0.0149	-2.587	p = 0.00973**

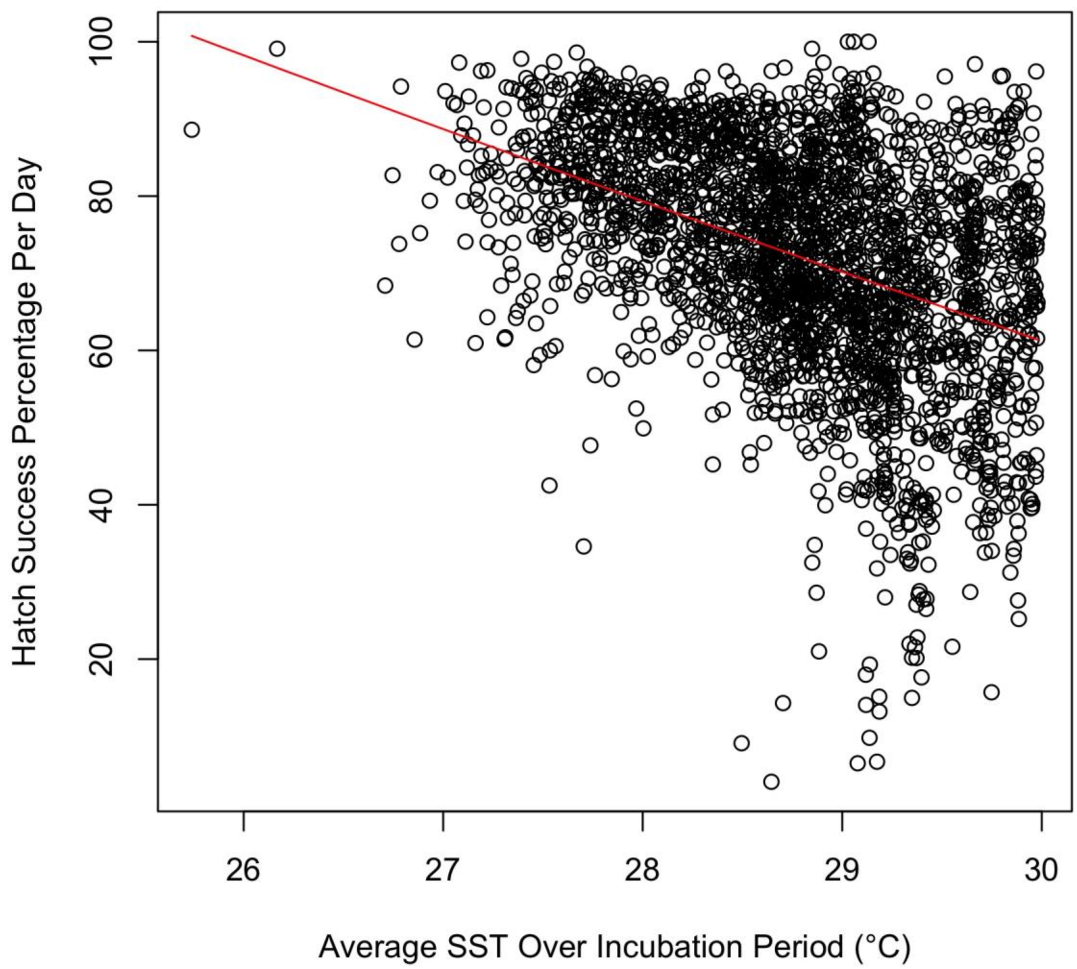

Figure 24: Hatch success percentage compared to average sea surface temperature over the average incubation period (°C).
Linear model: $y = -9.123X + 334.771$, $R^2 = 0.180$, $p < 0.001$

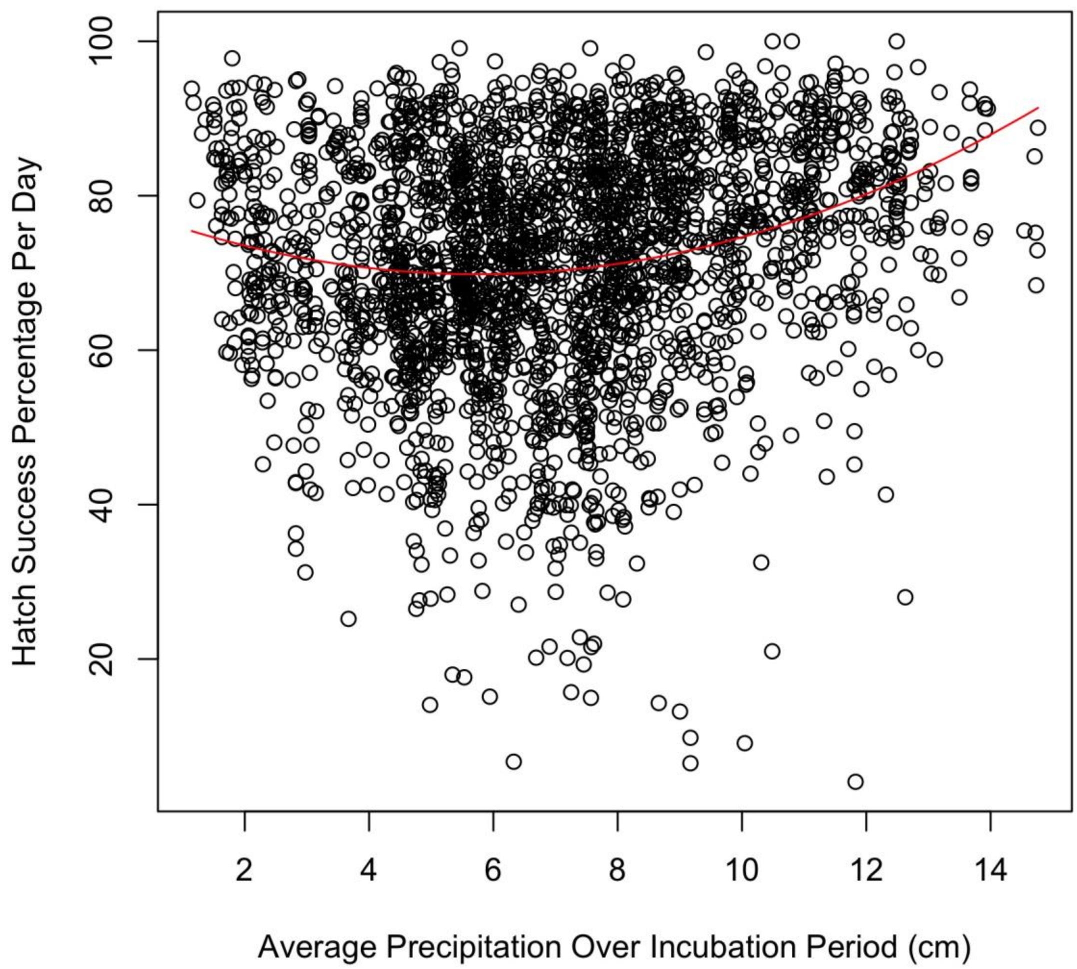

Figure 25: Hatch success percentage compared to average precipitation over the average incubation period (cm).
Polynomial model: $y = 0.265X^2 – 3.042X + 78.567$, $R^2 = 0.049$, $p < 0.001$

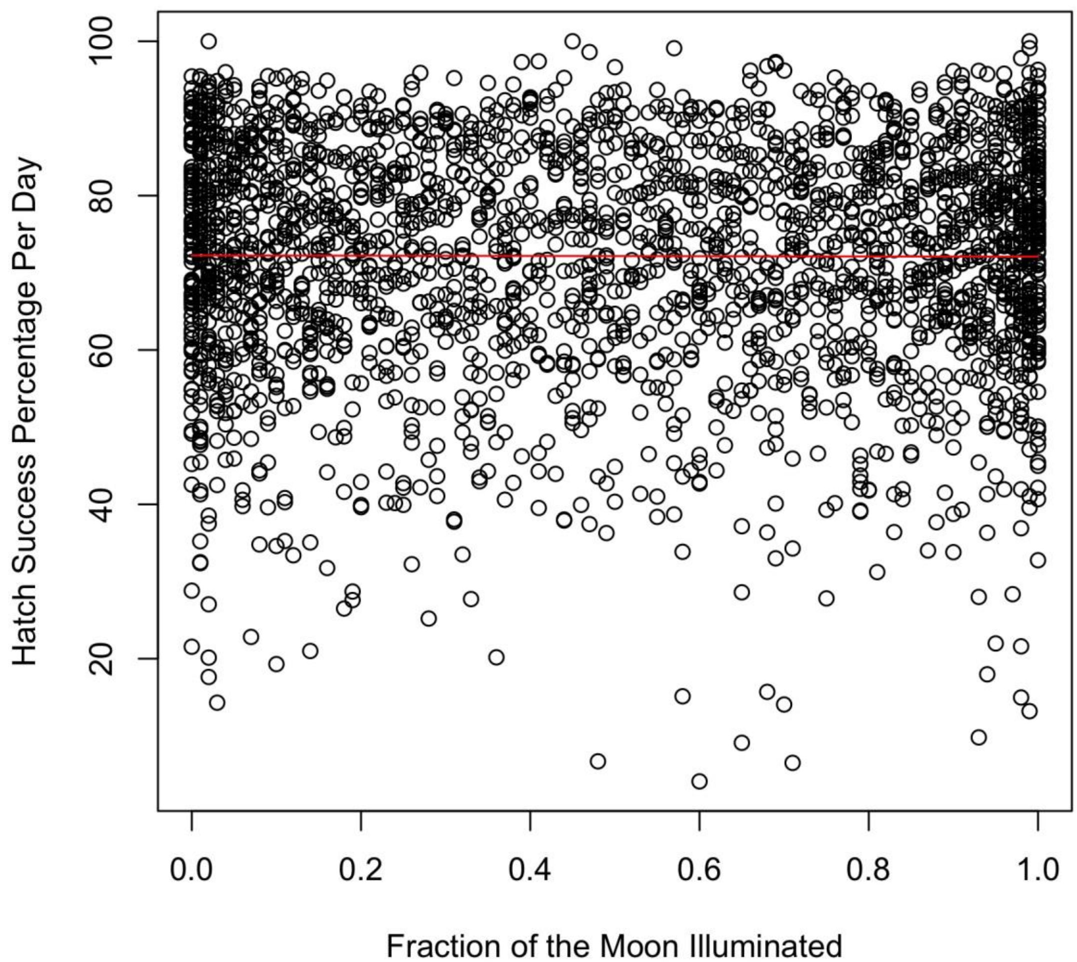

Figure 26: Hatch success percentage compared to lunar fraction on the hatch date. Linear model: $y = -0.164X + 72.250$, $R^2 = 0.0000151$, $p = 0.845$

Table 5: Coefficients for the most parsimonious polynomial regression model describing loggerhead sea turtle hatch success percentages with respect to air temperature, sea surface temperature, and precipitation over the incubation period, plus daily values of air temperature, sea surface temperature, and lunar fraction, as well as their interactions. Asterisks indicate the level of statistical significance.
R^2 = 0.307, p < 0.001

Coefficients	Estimate	Std. Error	T Value	P Value
Intercept	1,336,000	358,600	3.726	p < 0.001***
Lunar Fraction	-757.5	255.6	-2.964	p = 0.00307**
Incubation Air Temperature	-140,900	29,980	-4.699	p < 0.001***
I (Incubation Air Temperature)	2,308	536.7	4.301	p < 0.001***
Daily Air Temperature	36,450	10,470	3.481	p < 0.001***
I (Daily Air Temperature^2)	-652.1	188.5	-3.459	p < 0.001***
Incubation Precipitation	-2,437	637.6	-3.821	p < 0.001***
I (Incubation Precipitation^2)	176.4	44.38	3.974	p < 0.001***
Incubation SST	26,670	8,105	3.291	p = 0.00101**
I (Incubation SST^2)	-960.3	166.9	-5.754	p < 0.001***
Daily SST	-114,500	28,120	-4.071	p < 0.001***
I (Daily SST^2)	1,982	490.6	4.040	p < 0.001***
Lunar Fraction : Daily Air Temperature	54.88	18.33	2.994	p = 0.00278**
Lunar Fraction : I (Daily Air Temperature^2)	-0.992	0.328	-3.021	p = 0.00255**
Incubation Air Temperature : Incubation Precipitation	178	46.05	3.865	p < 0.001***
Incubation Air Temperature : I (Incubation Precipitation^2)	-12.89	3.214	-4.011	p < 0.001***
Incubation Air Temperature : Incubation SST	612.3	95.56	6.407	p < 0.001***
Incubation Air Temperature : I (Incubation SST^2)	-10.58	1.656	-6.391	p < 0.001***
Incubation Air Temperature : Daily SST	938.5	2,088	4.496	p < 0.001***
Incubation Air Temperature : I (Daily SST^2)	-166.8	36.20	-4.609	p < 0.001***
I (Incubation Air Temperature^2) :	-3.253	0.831	-3.916	p < 0.001***

Incubation Precipitation				
I (Incubation Air Temperature^2) : I (Incubation Precipitation^2)	0.236	0.058	4.061	$p < 0.001$***
I (Incubation Air Temperature^2) : Daily SST	-164.1	37.19	-4.412	$p < 0.001$***
I (Incubation Air Temperature^2) : I (Daily SST^2)	2.917	0.644	4.527	$p < 0.001$***
Daily Air Temperature : Incubation SST	-1,244	554	-2.245	$p = 0.0249$*
Daily Air Temperature : I (Incubation SST^2)	21.73	9.683	2.244	$p = 0.0249$*
Daily Air Temperature : Daily SST	-1,300	645.4	-2.015	$p = 0.0440$*
Daily Air Temperature : I (Daily SST^2)	22.61	11.15	2.028	$p = 0.0426$*
I (Daily Air Temperature^2) : Incubation SST	22.10	10.10	2.189	$p = 0.0287$*
I (Daily Air Temperature^2) : I (Incubation SST^2)	-0.386	0.176	-2.189	$p = 0.0287$*
I (Daily Air Temperature^2) : Daily SST	23.40	11.54	2.028	$p = 0.0427$*
I (Daily Air Temperature^2) : I (Daily SST^2)	-0.0407	0.199	-2.042	$p = 0.0413$*
Incubation Precipitation : I (Incubation Precipitation^2)	-0.0177	0.00849	-2.080	$p = 0.0377$*
Incubation SST : I (Incubation SST^2)	13.35	1.554	8.595	$p < 0.001$***
Incubation SST : Daily SST	235.3	79.00	2.978	$p = 0.00293$**
I (Incubation SST^2) : Daily SST	-9.955	2.401	-4.145	$p < 0.001$***
I (Incubation SST^2) : I (Daily SST^2)	0.0103	0.0244	4.247	$p < 0.001$***

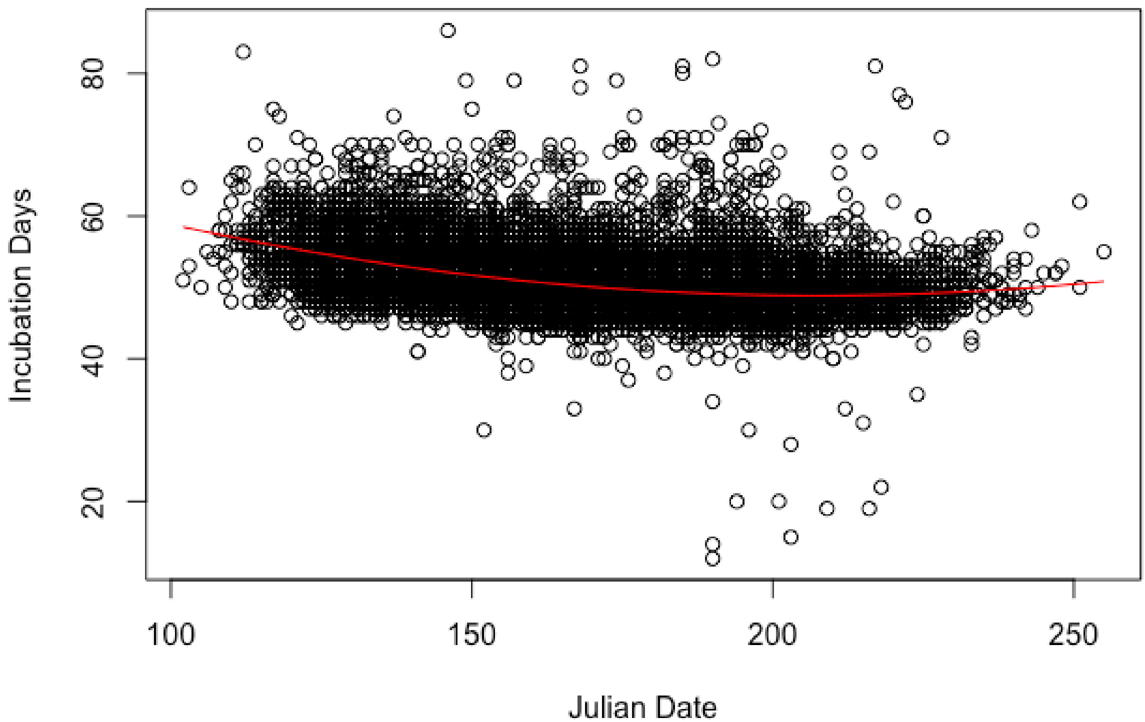

Figure 27: Nest lay date compared to total length of the incubation period. Polynomial model: $y = 0.000866X^2 - 0.359X + 86.08$, $R^2 = 0.204$, $p < 0.001$

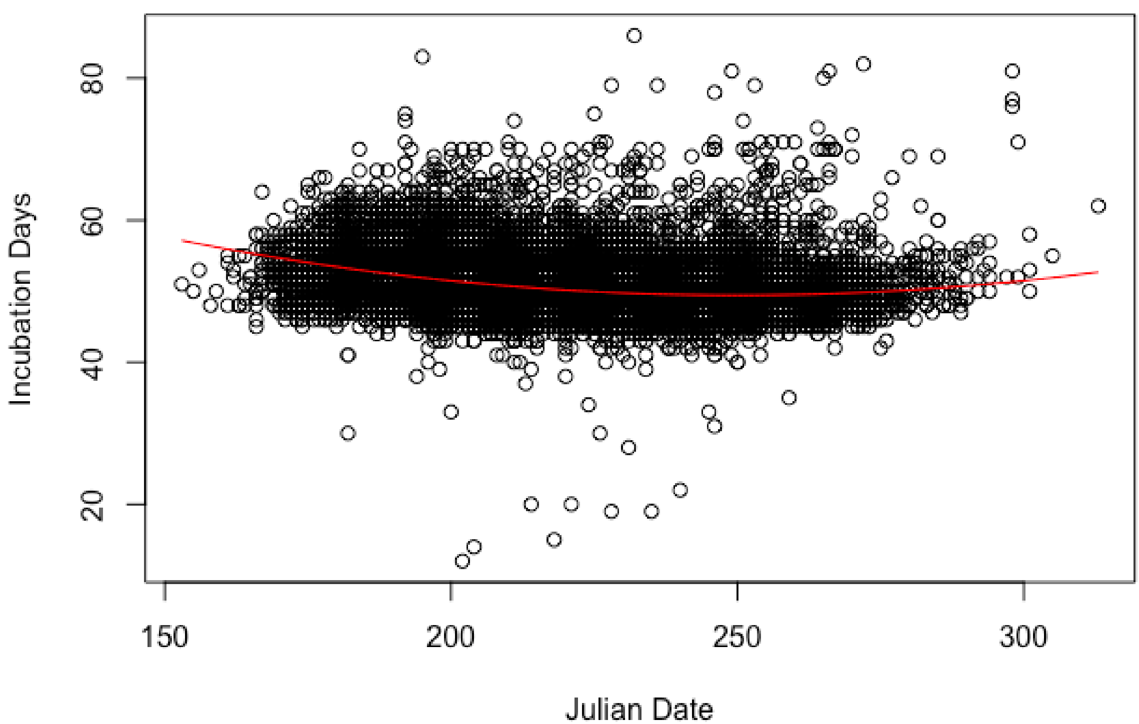

Figure 28: Nest hatch date compared to total length of the incubation period. Polynomial model: $y = 0.000821X^2 - 0.410X + 100.7$, $R^2 = 0.103$, $p < 0.001$

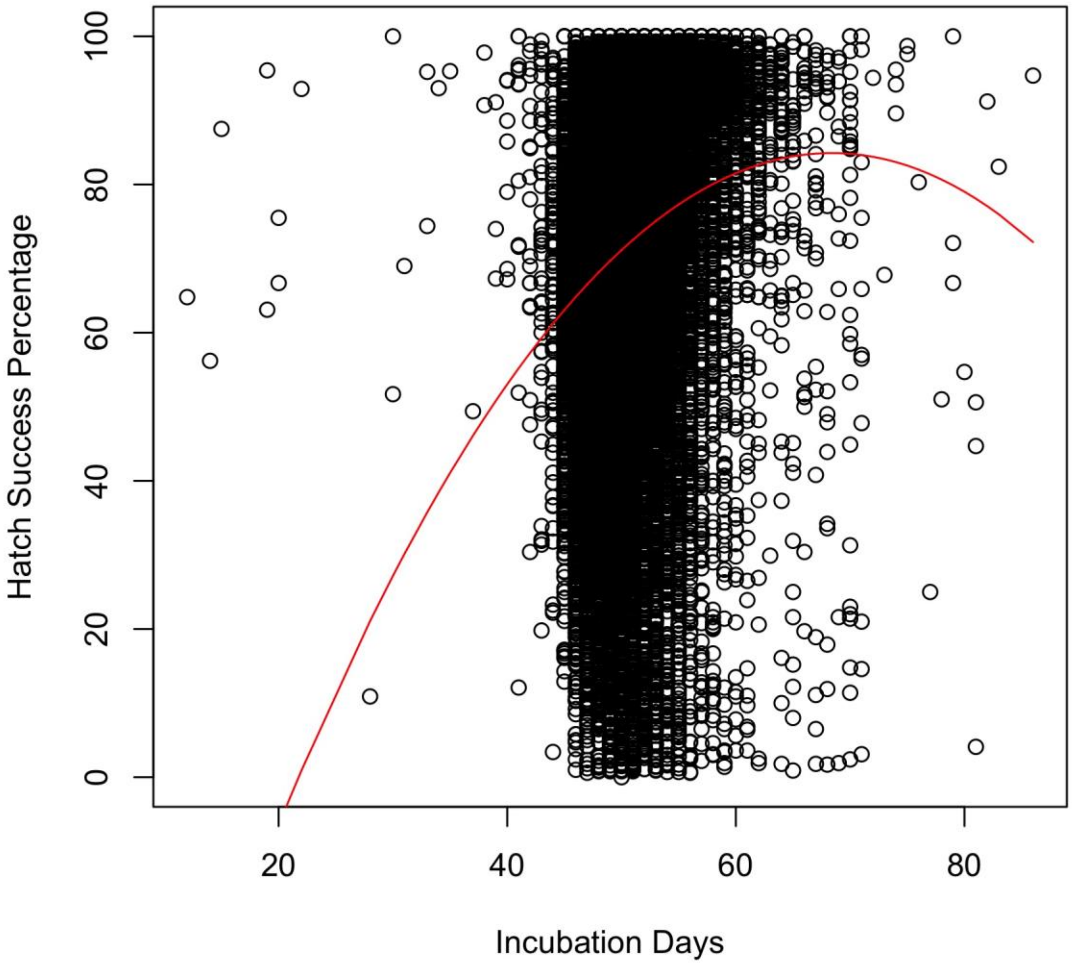

Figure 29: Total length of the incubation period compared to hatch success percentage. Polynomial model: $y = -0.039X^2 + 5.296X - 96.862$, $R^2 = 0.044$, $p < 0.001$

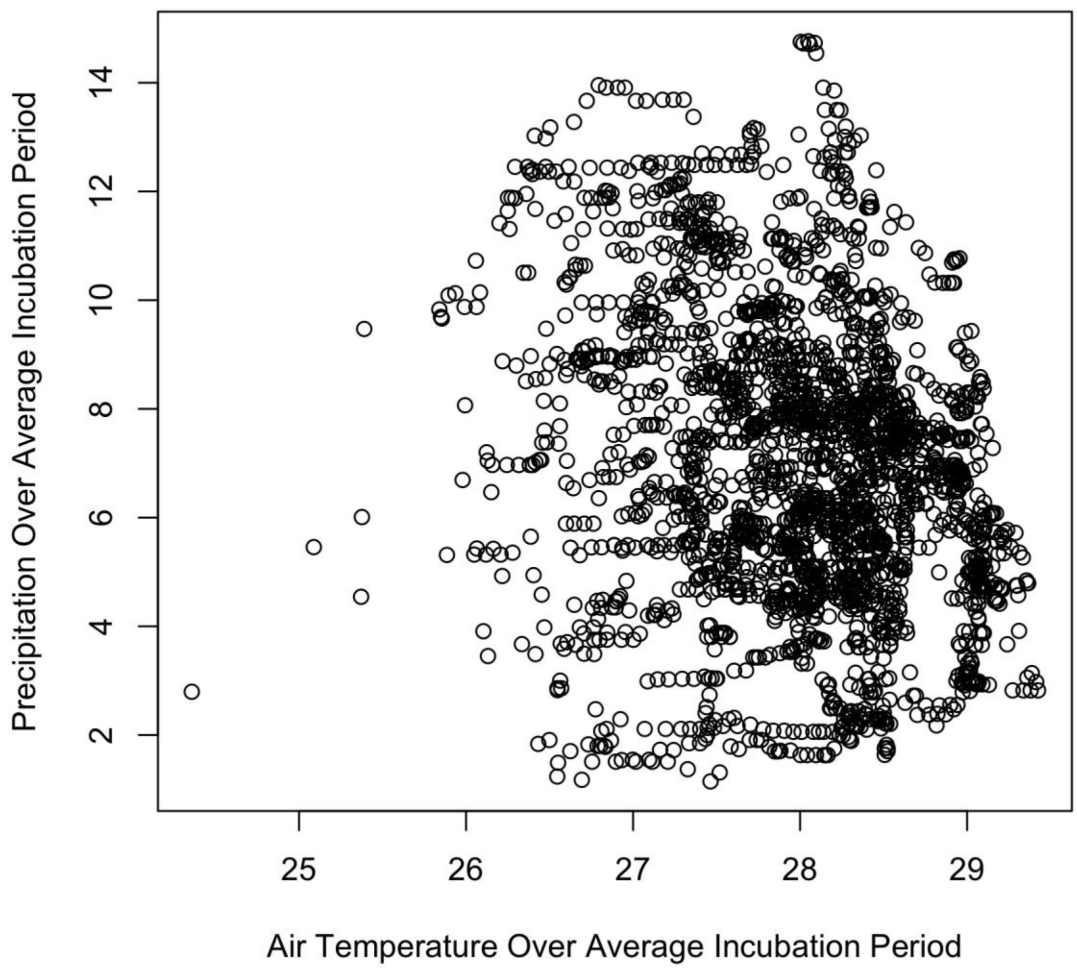

Figure 30: Air temperature (°C) compared to precipitation over the incubation period (cm). Correlation: p < 0.0001, tau = -0.157

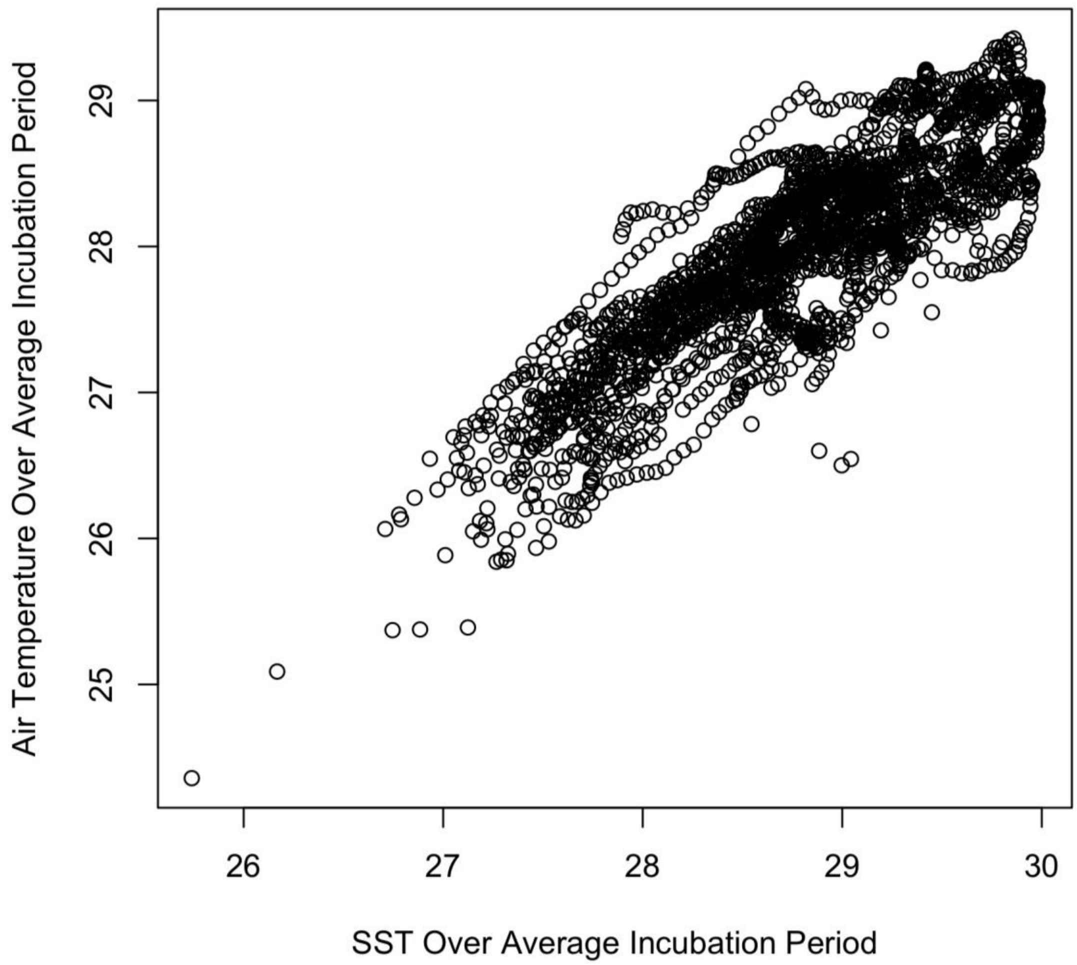

Figure 31: Sea surface temperature (°C) compared to air temperature over the incubation period (°C).
Correlation: $p < 0.001$, tau = 0.649

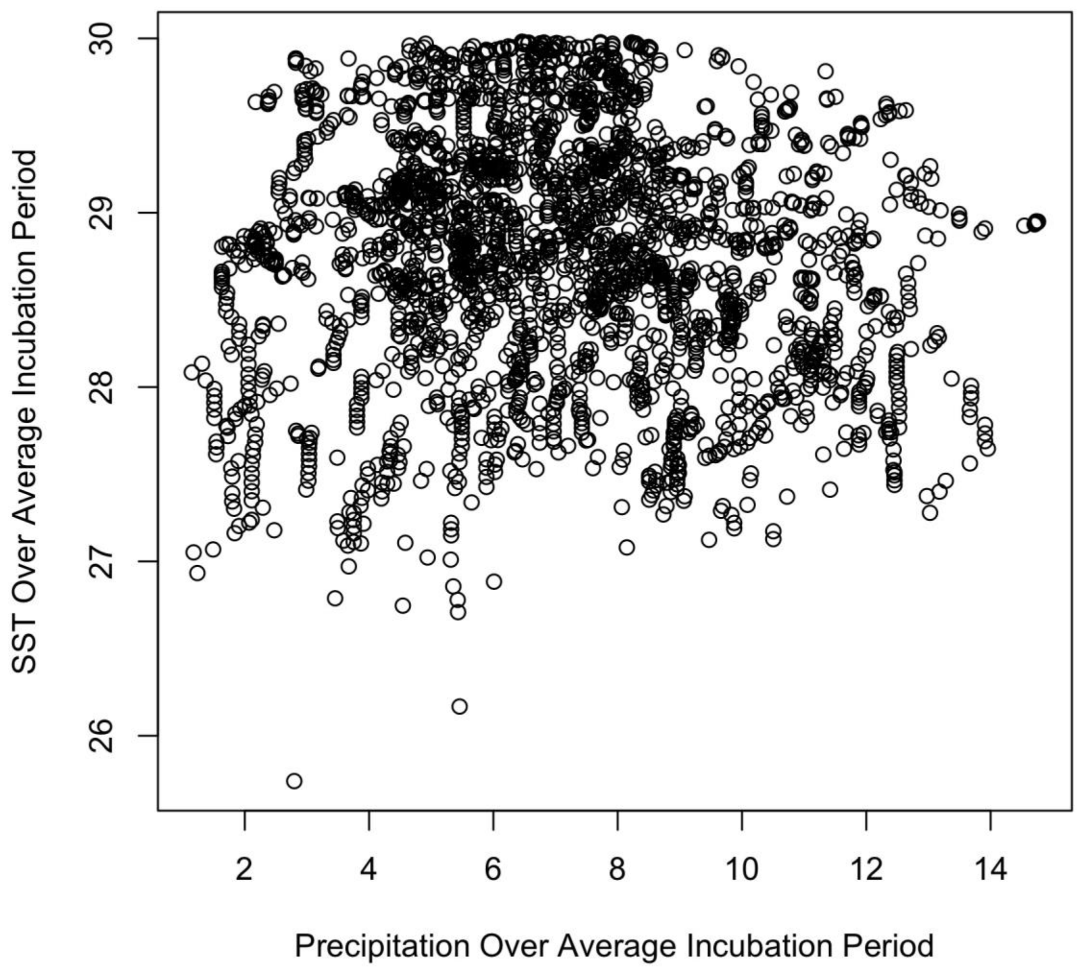

Figure 32: Precipitation (cm) compared to sea surface temperature over the incubation period (°C). Correlation: $p < 0.001$, tau = -0.0514